

FINAL REPORT

Methods for Assessment of Species Richness and Occupancy
Across Space, Time, Taxonomic Groups, and Ecoregions

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List of acronyms

AIC. Akaike's Information Criterion.

CI. Confidence interval or credible interval.

CV. Coefficient of variation.

DEM. Digital elevation model.

DoD. Department of Defense.

GIS. Geographic information system.

HUC. Hydrological Unit Classification.

LANDFIRE. Landscape Fire and Resource Management Planning Tools Project.

NAIP. National Agriculture Imagery Program.

PRISM. Parameter–elevation Relationships on Independent Slopes Model.

SD. Standard deviation.

SDM. Species distribution model.

SE. Standard error.

Keywords

anurans, birds, butterflies, Chesapeake Bay Lowlands, Great Basin, detection probability, indicator species, occupancy, species richness

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Abstract

Objectives

We aimed to develop and evaluate practical methods to estimate species richness and occupancy of diverse taxonomic groups across space and time and in diverse ecosystems. As reflected in the statement of need to which this project responded, our work is relevant to the needs of the Department of Defense (DoD) to assess and monitor native species and to evaluate the potential effects of land use and management actions on native species. Species richness, or the number of native species, is a common surrogate measure of ecosystem status. Occupancy, the probability that a given location is occupied by a species, can serve as a surrogate measure of the species' abundance, which in turn is related to probability of persistence.

This project addressed five major objectives consistent with the primary aim. First, we assessed relations between environmental variables and species richness at nested spatial extents. Second, we developed guidelines for periodicity of sampling. Third, we tested methods for estimating species richness of multiple taxonomic groups on the basis of spatial variation in occurrence or heterogeneity of one group. Fourth, we examined the extent to which occupancy could provide a foundation for measuring species richness. Fifth, we investigated potential responses of species richness and occupancy to manageable environmental changes, and meaningful scales of sampling for detection of biological effects of environmental change.

Technical approach

As land use changes in the multi-jurisdictional lands surrounding DoD installations in the United States, it becomes more challenging to sustain military readiness and conserve biological diversity. We sampled anurans, birds, and butterflies in the Chesapeake Bay Lowlands (including Joint Base Langley–Eustis), and birds and butterflies in the central and western Great Basin (including Hawthorne Army Depot and the Marine Corps Mountain Warfare Training Center), from 2012–2015. Working in ecosystems in which land-cover configurations and drivers of those configurations differ, and on disparate faunal groups, allowed us to evaluate the geographic and taxonomic transferability of our methods and inferences. We also capitalized on existing data and local experience that served the project aims.

Our sampling methods allowed us to estimate detection probability—the probability of detecting a species if it is present. If detection probability is not quantified, inferred relations between environmental covariates and species occurrence or demography may be erroneous. We conducted hierarchical analyses of the species richness of birds and butterflies in the central and western Great Basin. We modeled species richness at two nested spatial extents as functions of environmental variables measured at either extent. We used the same data to develop a method to identify indicator species (small sets of species with occurrence patterns that are related to species richness of larger sets) and environmental variables that explain considerable variation in species richness. We conducted novel, rigorous external evaluations of the spatial and temporal transferability of such indicator species. Furthermore, we evaluated the extent to which different ecological processes might drive spatial and temporal variation in species identities.

We examined the responses of estimated detection probability and occupancy of birds in the Chesapeake Bay Lowlands and central and western Great Basin to the duration of sampling. Additionally, we examined whether detection probability and occupancy of birds and anurans in the Chesapeake Bay Lowlands, and butterflies in the Great Basin, differed if sites were sampled repeatedly on a single day versus once each on multiple days.

We explored the extent to which occupancy of butterflies in the Chesapeake Bay Lowlands and central and western Great Basin was associated with vegetation structure and composition, topography, and other environmental attributes and whether assumptions of closure were met with assemblage-level sampling designs. Furthermore, we identified attributes of wetlands and the surrounding terrestrial environment that were associated with anuran populations of high relative abundance versus populations of any abundance class, and evaluated how these attributes relate to different life history stages.

We examined how songbirds in the Chesapeake Bay Lowlands, including species of concern, may respond to changes in vegetation fragmentation and structure that result from urbanization and different levels of use by white-tailed deer. We also explored turnover in species composition of birds and butterflies in the central and western Great Basin to gain insight into meaningful scales of sampling for detection of biological effects of environmental change.

Results

In the central and western Great Basin, species richness of birds and butterflies responded to environmental variables at different spatial extents. Species' identities were more consistent in space in butterfly than in bird assemblages, whereas spatial nestedness (the extent to which species-poor faunas are statistical subsets of species-rich faunas) often was higher in butterfly than in bird assemblages. In some cases, we were able to explain more than 80% and 70% of the variation in species richness of birds and butterflies, respectively, as functions of vegetation and topography. The predictive accuracy and spatial and temporal transferability of models of species richness of birds and butterflies that are based on indicator species can exceed that of models based on environmental variables.

In all of our ecosystems, modest increases in the duration of point counts for birds did not affect inferences based on occupancy models, but might affect estimates of species richness that were not detection-weighted. Given our results, we believe that estimation of use may be equally or more informative than estimation of occupancy for exploring species-environment relations.

In many cases, because detection probabilities for many species of birds and butterflies were low, occupancy could not be estimated for more than 50% of the species detected in each ecosystem and year. Although imperfect detection may lead to biased estimates of species occurrence, demographic parameters, and species-environment relations, achieving certain scientific objectives still may require use of occurrence data that are not detection weighted. Our results suggest that if anurans are extirpated from wetlands in the Chesapeake Bay Lowlands, the wetlands are unlikely to be recolonized.

Benefits

We regularly shared data and inferences with environmental managers at the installations on which we worked, who indicated that our results would contribute to watershed management programs and Integrated Natural Resources Management Plans. We also shared data and inferences with DoD partners, including Landscape Conservation Cooperatives. In the Chesapeake Bay Lowlands, our results are relevant to management of white-tailed deer, which have substantial effects on other native species and, via transmission of disease vectors, public health. In the Great Basin, our results are applicable to vegetation treatments that are intended to increase the probability of persistence of Greater Sage-Grouse and benefit hundreds of other species. Our results also suggest directions for future research on the extent to which simple measures of species occurrence may provide information on probabilities of species persistence.

Objective

The desired outcomes of the statement of need to which this project responded were knowledge that improves understanding of assessment, monitoring, and management of native species at multiple spatial and temporal scales; knowledge that can assist resource managers in providing effective and cost-efficient methods for accomplishing such assessment and monitoring and for projecting the effects of land use and management actions; knowledge that addresses diverse aspects of theory related to assessment and monitoring of native species and its application (including the fact that habitat is species-specific, and therefore different species will have different responses to environmental change); and knowledge that promotes assessment and monitoring of native species within and among land management and administrative units. Assessment and monitoring of native species is relevant to the Department of Defense (DoD) because maintenance of these species can conflict with operations that sustain military readiness; because the DoD is committed to environmental stewardship; and because the DoD must comply with laws that protect species and other levels of biological diversity. Furthermore, information on where and when species of concern occur, and associations between those species and their environment, often is necessary to inform environmental management on installations.

In response to the statement of need, the objective of this project was to develop and validate practical methods to estimate species richness and occupancy across space and time. We define species richness as the number of native species in a given location during a given time period. Occupancy, the probability that a given location is occupied by a species, is a state variable that can serve as a surrogate measure of the abundance of that species (MacKenzie and Nichols 2004). Abundance and geographic distribution are strongly related to probability of persistence (Lande 1993, Foley 1994, Harris and Pimm 2008). We aimed to develop or refine methods that facilitate estimation of a species' spatial pattern of occupancy, detect changes in its distribution, and make inference to its probability of regional persistence. We also aimed to develop methods that were statistically rigorous; transferable in space (including within and among ecosystems) and time; where possible, transferable among taxonomic groups; and that reconciled statistical rigor with biological realism. We quantified the extent to which occupancy of three faunal groups in three ecosystems (including two biogeographic subregions of one extensive ecoregion) can be explained as a function of geophysical attributes, land cover, and the composition and structure of vegetation at multiple spatial extents and resolutions. We sampled birds, butterflies, and anurans in the Chesapeake Bay Lowlands (including Joint Base Langley–Eustis), and birds and butterflies in the central and western Great Basin (including Hawthorne Army Depot and the Marine Corps Mountain Warfare Training Center). We are continuing to use the results to project how occupancy and species richness may change in response to environmental changes that are responsive to management. We are providing all data and customized summaries to DoD resource managers and environmental specialists, and installations indicated that they will incorporate our results into watershed management programs and Integrated Natural Resources Management Plans.

At the start of the project, we had five major tasks that responded to the statement of need. Our first objective was to assess two methods for correcting bias in estimates of species richness at small spatial extents: standardizing sampling effort by area sampled and by number of individuals sampled. Over the course of the project, as described below, we refocused this

objective and conducted a hierarchical estimation of species richness of birds and butterflies in the central and western Great Basin. Our second objective was to develop guidelines for periodicity of sampling. We used data on anurans from the Chesapeake Bay Lowlands and birds and butterflies from the Chesapeake Bay Lowlands and central and western Great Basin to address this objective. Third, we used data on birds and butterflies from the central and western Great Basin to test methods for estimating species richness of multiple taxonomic groups on the basis of spatial variation in occurrence or heterogeneity of a single taxonomic group. Our fourth objective was to develop a structured method for species-level monitoring that used occupancy as a surrogate measure of abundance for estimating patterns of species richness. We used data on anurans and on birds and butterflies from the Chesapeake Bay Lowlands and central and western Great Basin to address that objective. Fifth, we aimed to model potential responses of species richness and occupancy to environmental change. In the Chesapeake Bay Lowlands, we focused on responses of birds to urbanization and to the density of white-tailed deer (*Odocoileus virginianus*), the abundance of which has increased by more than 3000% over the past century. Rapid increases in the regional abundance of white-tailed deer have been linked not only with changes in native flora and fauna but with increases in the incidence of tick-borne diseases that affect humans, such as Lyme disease. The abundance and density of deer can be managed by humans both within and beyond installation boundaries. In the central and western Great Basin, our results are applicable to planned management treatments on DoD and other public lands, such as manipulations of vegetation that are intended to increase the probability of persistence of Greater Sage-Grouse (*Centrocercus urophasianus*) and benefit more than 350 other species of animals (BLM 2015, USFS 2015).

Background

Species richness commonly is used as a surrogate measure of the status of an ecological system, and it is a measure readily understood by decision-makers and the public. Therefore, species richness long has been a focus of assessment and monitoring. However, species richness alone is insufficient to characterize whether locations are likely to sustain species and ecological function over the long term. Additionally, most measures of species richness are not accurate statistical estimates because it is impossible to determine their precision or the effects of possible biases, such as underestimation of species richness as a result of not detecting rare or cryptic species. Nevertheless, assessments of numerous individual species, especially when density or abundance is the state variable, generally have been considered too complex and expensive to be feasible.

Until the early 2000s, most methods for estimating species richness, abundance, and demographics of plant and animal populations did not account for detection probability—the probability of detecting a species at a given location conditional on its presence. If detection probability is not quantified, estimators of presence, abundance, and other measures of population dynamics may be biased and may lead to erroneous inferences about relations between response variables and environmental covariates (Gu and Swihart 2004, MacKenzie 2005). Many sampling and analytical methods have been developed to address the reality of imperfect detection (e.g., Buckland et al. 2001, Williams et al. 2002). For example, the single-season occupancy model (MacKenzie et al. 2002) was developed to account for the possibility of false absences—species that are present, but not detected, during a given sampling period—in estimating species' spatial or temporal distributions (MacKenzie et al. 2006). There is a solid theoretical basis for using occupancy as a surrogate measure of a species' abundance or state (e.g., reproductive status) (He and Gaston 2003, Nichols et al. 2007, Green et al. 2011). Abundance, in turn, is strongly related to probability of persistence (Gaston et al. 2000, Zuckerberg et al. 2009), and maximizing the probability of species persistence commonly is a high priority for federal and state managers of natural resources.

Use of occupancy models has been advocated not only on the basis of statistical rigor, but on the basis of feasibility. The data required to estimate demographic parameters or abundance precisely, especially for relatively rare species, can be expensive and difficult to obtain (MacKenzie et al. 2004, Corbani et al. 2014). Because occupancy models do not rely on captures or detections of multiple individuals in a population, they can be applied to a greater proportion of the species in a community. Researchers have used occupancy models to estimate species richness (Kéry et al. 2009, Dorazio et al. 2010, Carillo-Rubio et al. 2014), trends in distribution (van Strien et al. 2013, Weir et al. 2014), and extinction–colonization dynamics (Fernández-Chacón et al. 2014, Pearson et al. 2015) of multiple taxonomic groups. To model occupancy, one selects a sample of sites (e.g., quadrats or habitat patches) and surveys each site multiple times in a given season or year (MacKenzie et al. 2002). Multiple surveys are necessary to estimate detection probability, and the number and timing of these surveys is a major consideration in the study design.

There are four core assumptions of occupancy models. First, occupancy at a site does not change among surveys (i.e., the closure assumption). Second, either there is no heterogeneity in probabilities of detection and occupancy of a given species, or heterogeneity is effectively

modeled. Third, detections of a given species are independent among surveys and sites. Fourth, the species of interest are not falsely detected (MacKenzie et al. 2006). The closure assumption arguably is the most challenging. The occupancy status of mobile organisms on sample units rarely is constant across the season, and changes in occupancy may not be random. Therefore, detection estimates that treat multiple surveys as replicate samples of the same species may be negatively biased, and the resulting estimates of occupancy positively biased. One possibility is to sample each site repeatedly on each sampling date (the robust design; Kendall et al. 1997). Another option is to relax the closure assumption by assuming that species are available for sampling at different times (Kendall et al. 2013). We explored both of these options in our work. We examined trade-offs between single-day and multiple-days sampling of anurans and birds in the Chesapeake Bay Lowlands and butterflies in the central and western Great Basin, and we tested whether different species of butterflies in our three ecosystems met the assumption of closure.

Working in ecosystems in which land-cover configurations and drivers of those configurations differ allowed us to evaluate the transferability of our methods and inferences. For example, patches of deciduous forest in the Chesapeake Bay Lowlands are relatively dispersed, whereas patches of pinyon and juniper woodland in the Great Basin are relatively clumped; riparian land-cover generally is more extensive and less fragmented in the mesic Chesapeake Bay Lowlands than in the arid Great Basin. Outside of installations, which have relatively contiguous land cover, most of the Chesapeake Bay Lowlands is dominated by heavily fragmented private holdings, whereas the Great Basin is dominated by multijurisdictional federal lands.

Throughout the mid-Atlantic region, including the Chesapeake Bay Lowlands, fragmentation of deciduous forest is driven by urban, exurban, and rural settlement, including construction of roads and other infrastructure; by agriculture; and by development of coal and wind energy (Woolmer et al. 2008). In contrast, fragmentation of woodlands in the Intermountain West, including the Great Basin, is driven both by natural processes such as wildfire and by land uses such as domestic livestock grazing, energy development (wind, solar, oil, gas, and thermal), and exurbanization, with associated infrastructure such as secondary roads. Secondary roads cover 1.1% of the area in the western United States and are third most extensive anthropogenic feature in that region (following agriculture [9.8%] and populated areas [1.9%]; Leu et al. 2008) and demonstrably affect invasion by non-native plants and the number of point sources of fires (Gelbard and Belnap 2003).

Hierarchical estimates of species richness

We originally aimed to assess two methods for correcting bias in estimates of species richness at small spatial extents: standardizing sampling effort by area sampled and by number of individuals sampled. The relation between species richness and area often has one of two functional forms: a power function (linear on a plot of $\log[\text{species richness}]$ against $\log[\text{area}]$) or an exponential function (linear on a plot of species richness against $\log[\text{area}]$). At least five biological mechanisms have been hypothesized to explain relations between species richness and area. The habitat diversity hypothesis suggests that as area increases, the number of niches increases. The area hypothesis is based on the fact that probability of extinction generally

decreases as abundance increases, and abundance generally increases as area increases. The passive sampling hypothesis assumes that immigration of a given species increases as area increases. The resource concentration hypothesis suggests that resource density increases as area increases. The edge effects hypothesis notes that the perimeter-to-area ratio typically decreases as area increases.

Most published species richness-area curves were based on one of four sampling designs (Figure 1). Nested quadrats accumulate area by embedding each quadrat in a quadrat of equal proportions but larger size. Grids are contiguous sample units of the same size and shape; area is accumulated by increasing the number of cells sampled. Non-contiguous quadrats are a regular array of sample units of the same size and shape, typically homogenous and embedded in a homogenous matrix. Island-like patches are of different size and shape, typically embedded in a homogenous matrix.

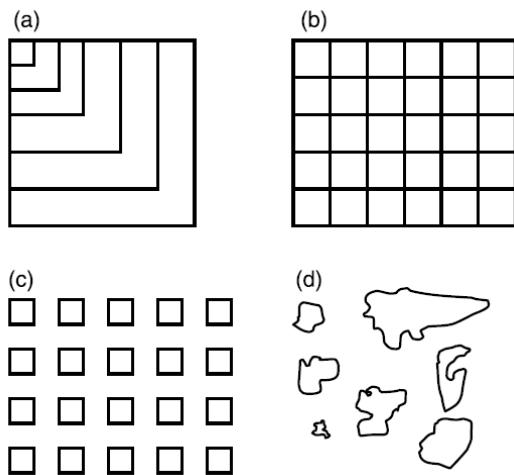


Figure 1. Sampling designs for species richness-area curves: nested quadrats (a), grid (b), non-contiguous quadrats (c), island-like habitat patches (d).

Species richness-area plots based on quadrat sampling designs may reach the same asymptote, but the number of quadrats necessary to reach the asymptote decreases as quadrat size increases. Thus, species-area relations are affected by both the spatial extent and resolution of sampling.

As we pursued this objective, we realized that some of our sampling designs differed from those typically represented in the literature, which made it difficult to apply existing species richness-area models. We sampled anurans in island-like patches in a heterogeneous matrix. However, the regional species pool of anurans is relatively well-known, and rarefaction resulted in estimates of species richness that considerably exceeded that of the species pool. Therefore, it did not make sense to apply species richness-area models to anurans. We sampled birds in all ecosystems in heterogeneous patches of equal size and shape that were embedded in a heterogeneous matrix. We sampled birds in this manner because point-count surveys are the most common method of sampling birds (see next section); conducting point-count surveys will allow our data to be incorporated into numerous other analyses that also are based on point counts. Additionally,

because land cover and topography in the ecosystems in which we worked is highly heterogeneous, it was not possible to establish a sampling array of homogenous patches in a homogenous matrix. We also sampled butterflies in the Chesapeake Bay Lowlands in heterogeneous patches of equal size and shape that were embedded in a heterogeneous matrix. We sampled butterflies in the central and western Great Basin in heterogeneous patches of unequal size embedded in a heterogeneous matrix. Our sampling design for butterflies in the central and western Great Basin allowed us to pool data from the current project with data collected in previous years (this was not a consideration for collection of butterfly data in the Chesapeake Bay Lowlands). The latter sampling design also was developed to accommodate extensive elevational gradients in the Great Basin, which our previous work suggested were associated with species richness and species occurrence.

Therefore, we developed both novel data-aggregation methods and novel statistical methods to address species richness-area relations in our data. These methods also allowed us to explore relations between species richness and environmental gradients other than area, such as elevation or topographic heterogeneity, that may explain considerable variation in species richness. The ability to address other environmental gradients is highly relevant given landscape heterogeneity; that is, other environmental attributes cannot be held constant while area varies.

Periodicity of sampling: duration of point counts of birds

Our second objective was to develop guidelines for periodicity of sampling. Point-count surveys are the most common method of sampling birds (Rosenstock et al. 2002, Bart 2005, Buckland 2006), and many investigators have examined whether species- or community-level inferences derived from point counts are affected by sampling design (e.g., Ralph et al. 1993, 1995, Petit et al. 1995, Smith et al. 1995, Thompson and Schwalback 1995, Bibby et al. 2000, Shiu and Lee 2003, Esquivel and Peris 2008, Cimprich 2009, Reidy et al. 2011). The temporal window for effectively sampling birds on a given day can be relatively short, sometimes less than four hours, and the breeding season in a given region is often limited to five to eight weeks. Therefore, there are trade-offs among the number of point-count locations (hereafter points; Buskirk and McDonald 1995) sampled, the geographic extent of sampling, and the duration of point-count surveys (hereafter counts; Buskirk and McDonald 1995, Ralph et al. 1995, Vergara et al. 2010).

Estimates of detection probability and abundance generally increase as count duration increases, but there is considerable variation among species. For example, detection probabilities of 14 songbird species that breed in deciduous forests in the eastern United States increased from > 0.4 to > 0.9 when count duration increased from 5 min to 20 min. However, detection probabilities of 57% of these species varied among years (Dawson et al. 1995). Similarly, detection probability increased as count duration increased from 3 to 6 to 10 min for six songbird species that breed in deciduous forests in the eastern United States (Buskirk and McDonald 1995). By contrast, mean abundance derived from 10-min counts was higher than that derived from 6-min counts for 15% of 13 species (Thompson III et al. 2002). Other studies found that the number of individuals increased as count duration increased regardless of the period during the morning in which 3-, 6-, or 10-min counts were conducted (Buskirk and McDonald 1995) or the time of year in which 5-, 10-, 15-, or 20-min counts were conducted (Smith et al. 1998). In southwestern

France, the abundance of 90% of 21 breeding species was greater when based on 10-min than 5-min counts; the abundance of all 21 species was greater when based on 20-min than 15-min counts (Bonthoux and Balent 2012). Estimates of the density of tropical species that were adjusted for imperfect detection were 13% greater when based on 10-min than 2-min counts (Lee and Marsden 2008).

Count models suggest that the effect of count duration on precision is equivocal. Precision on the basis of the coefficient of variation (CV) was homogenous among 6-, 8-, and 10-min counts (Thompson et al. 2002), and precision on the basis of the standard error (SE) was homogenous among 3-, 6-, and 10-min counts (Buskirk and McDonald 1995). By contrast, Smith et al. (1998) found that SE-based precision decreased as count duration increased in 5-min increments from 5 to 20 min. Although many studies investigated the effects of increasing count duration on inferences from models based on counts, it is unclear whether count duration affects inferences from occupancy models (MacKenzie et al. 2002).

Occupancy models (MacKenzie et al. 2002) frequently are implemented to analyze point-count data (e.g., Betts et al. 2008, Saracco et al. 2011, Frey et al. 2012). Typically, occupancy models use data from repeated surveys at multiple locations to infer the proportion of locations or area that is occupied by a given species and, optionally, the environmental attributes associated with occupancy. Assessments of trade-offs between the number of sampling locations and the number of surveys at each location have resulted in guidelines for sampling design (MacKenzie et al. 2002, MacKenzie and Royle 2005, MacKenzie et al. 2006, Bailey et al. 2007). The effect of count duration on inferences from occupancy models, however, has received relatively little attention.

We explored the effects of 5-min and 8-min count durations on inferences about detection probability and occupancy, and precision of occupancy estimates, during the breeding seasons of 2012 and 2013 in the Chesapeake Bay Lowlands, central Great Basin, and western Great Basin. To extend the comparison beyond two years, we also examined whether estimates of occupancy differed from 2009 through 2013 for three species in the central Great Basin (data collection from 2009 through 2011 was supported by other sources). Furthermore, we determined the percentage of species for which occupancy models converged, i.e., diagnostics indicated no problems with parameter estimation, and for which detection probabilities derived from both 5-min and 8-min counts were ≥ 0.3 . The 0.3 threshold was suggested as a reasonable means to minimize bias (i.e., deviation of estimated occupancy from the true occupancy value) in occupancy estimates (MacKenzie et al. 2002). We chose the 5-min count duration to be consistent with standard point-count protocols (Ralph et al. 1993, 1995; Matsuko et al. 2014). We chose the 8-min duration because a pilot survey in the Chesapeake Bay Lowlands revealed that about 94% of species were detected within 8 min and because 8 min was the maximum count duration at which no reduction in the number of points was necessary given logistic constraints and associated travel time between points in the central and western Great Basin. The geographic and temporal breadth of our analysis is novel, and our inferences are relevant to the design of surveys based on counts and estimates of species richness based on occupancy models (e.g., Iknayan et al. 2014).

Periodicity of sampling: trade-offs between single-day and multiple-days sampling

Many sampling and analytical methods have been developed to address imperfect detection (e.g., Buckland et al. 2001, Williams et al. 2002). The lag time between surveys is a key consideration in the design of occupancy studies. Generally, one either visits each site on multiple days and conducts a single survey on each visit (hereafter, the multiple-days design), or visits each site on one day and conducts multiple surveys on that day (hereafter, the single-day design; MacKenzie et al. 2006). Both the multiple-days and single-day designs have been used to sample animals in diverse ecosystems, although the multiple-days design is more common. The single-day design, for example, was used to develop species distribution models for birds that breed in forests of the eastern United States (Schwenk and Donovan 2011). The multiple-days design was used to examine mammalian responses to roads (Nicholson and Van Manen 2009), changes in occupancy of 12 anuran species from 2002–2006 (Walls et al. 2011), population declines in amphibians from 2002–2011 (Adams et al. 2013), avian responses to vehicular sound (Goodwin and Shriver 2011), and detection probabilities for butterflies (Pellet 2008). There are many variations on the single-day and multiple-days designs.

The degree to which species are falsely detected should not differ between the single-day and multiple visits designs because false positives reflect observer error (McClintock et al. 2010a and 2010b). The degree to which the assumptions of closure, heterogeneity in detection probability and occupancy, and independence among detections of a given species are met, however, likely differs between the single-day and the multiple-days designs, and these differences may affect estimates of detection and occupancy probabilities and their precision.

A single-day design is more likely to meet the closure assumption than the multiple-days design because all surveys are completed over a relatively short period of time (MacKenzie et al. 2006, Rota et al. 2009). For example, males of some bird species vacate territories early in the breeding season and establish new territories for the remainder of the breeding season (Newton 2000, Betts et al. 2008). If a species leaves a sample unit during the period of sampling, then the closure assumption is violated. Violation of the closure assumption will not necessarily cause bias in estimates of occupancy probability. If movements on and off sample units by the focal species occur at random, then bias in the estimator is expected to be minor (MacKenzie et al. 2006, Kendall and White 2009). However, if movements are Markovian (i.e., the presence of the focal species on the sample unit during one survey is conditional on its presence during previous surveys), then bias may be greater (MacKenzie et al. 2006, Kendall and White 2009).

Variation in environmental conditions (e.g., weather) may cause detection probability to differ among surveys at a given site or among sites (MacKenzie et al. 2006, Simons et al. 2007). Although survey-specific covariates can account for some of the heterogeneity, the use of a single-day design may cause more heterogeneity in detection probability among sites than the multiple-visit design. Consider a scenario in which 10 sites are surveyed on the first day of sampling under a single-day design and a set of 10 different sites are surveyed on the second day. If weather conditions differ between the two days in ways that affect detectability of the species, then detection probability at sites surveyed on the first day will differ from detection probability at sites surveyed on the second day. The occupancy model is analogous to capture-recapture models for closed populations (MacKenzie et al. 2002), and heterogeneity in capture probability

negatively biases estimators of abundance from capture-recapture models (Kendall 1999). Similarly, we expect that if the single-day design induces heterogeneity in detection probability among sites, then estimators of occupancy probability will be biased negatively (MacKenzie et al. 2006). When the multiple-days design is implemented, weather conditions and any associated detection biases are likely to differ both among sites and among surveys at a given site. Because all sites in the sample rarely can be surveyed on the same day, weather conditions are not replicated among sites. Nevertheless, conventional wisdom suggests that the multiple-days design is more likely than the single-day design to capture the range of potential weather conditions within the bounds of sampling constraints to which the population of sites is exposed during the season.

The multiple-days design is more likely to meet the assumption of independent observations than the single-day design because surveys typically are separated by a longer period of time. An observer is more likely to remember species detected during previous surveys at a site if relatively little time elapses between surveys, particularly if the same observer conducts all surveys. Whether surveys are independent can be tested by including information on previous detections (i.e., capture history or detection history) as a covariate in a model of detection probability, and examining whether detection probability was higher at sites where the species previously was detected (MacKenzie et al. 2006).

We used occupancy data on birds and anurans in the Chesapeake Bay Lowlands and butterflies in the Great Basin to compare estimates of occupancy probabilities that were based on data from the two designs. To evaluate potential mechanisms for differences in the estimates, we also examined estimates of detection probability, detection histories, and support for the detection-history model from either design.

Estimation of species richness of multiple taxonomic groups on the basis of a single group

As reflected in the statement of need to which our work responded, interest in identifying standard and affordable ways to estimate species richness—the number of species in a given location and time period—has been maintained for decades. Methods for estimating species richness on the basis of incidence or abundance data include rarefaction (Sanders 1968) and the Chao 1 (Chao 1984), Chao 2 (Chao 1987), and jackknife (Burham and Overton 1978, 1979) estimators. Several more-recent methods of estimating species richness capitalize on increases in computing power or the popularity of occupancy models. For example, stacked and joint species distribution models (SDMs) (Dubuis et al. 2011, Pollock et al. 2014) make use of single-species SDMs, which project probability of occurrence on the basis of environmental variables that are measured in the field or derived from remotely sensed data (Elith and Leathwick 2009). Multiple-season, multiple-species hierarchical Bayesian models (Gelman and Hill 2007, Dorazio et al. 2010) are another example of the many relatively new, computationally intensive methods that can be used to estimate species richness and to explain variation in occupancy as functions of environmental covariates, ideally predicting occupancy in space or time.

In contrast to these newer methods, over time, many researchers have attempted to identify a small set of species with occurrence patterns that are related to species richness of a larger set of

organisms—i.e., indicator species (Pearson 1994, Morrison et al. 2012). Others have defined indicator species as species that are characteristic of land-cover types or environmental conditions (e.g., Niemi and McDonald 2004, De Cáceres et al. 2010). The latter definition, and associated methods (e.g., Dufrêne and Legendre 1997), differ from those we use here.

If external evaluations suggest that the indicator species-based models accurately predict species richness, then it may be possible to monitor the occurrence of a small number of indicator species rather than conducting comprehensive species inventories. In many temperate ecosystems, the cost of sampling the occurrence of all species of certain taxonomic groups, such as passerines, is not appreciably greater than that of sampling a small subset of the group. For taxonomic groups that are more cryptic, monitoring a subset of an assemblage may be much more feasible than monitoring the full assemblage. Identification of indicator species can be simpler computationally than innovative but largely unproven methods such as the implementation of SDMs or hierarchical Bayesian models, and the relations between indicator species and species richness may be easier to interpret and to communicate to end-users.

We conducted work on indicator species in the central Great Basin before the current project was initiated. In that earlier work, we used objective statistical methods to identify butterflies and birds that could indicate species richness of the same taxonomic group or the other taxonomic group (Mac Nally and Fleishman 2002, 2004, Thomson et al. 2005, 2007). For example, a model based on the occurrence patterns of five species of butterflies explained 88% of the deviance of species richness of 56 butterfly taxa; when predictions of this model were confronted with new data from a nearby set of locations, more than 90% of the observed values fell within the 95% credible intervals of the predictions (Mac Nally and Fleishman 2004). In our previous work, we also built models with data on birds and butterflies that were collected from 1996–2003 in three mountain ranges in the central Great Basin, and used bootstrapping to conduct internal evaluations of the models. Furthermore, in our previous work, we used new data on birds, collected in 2004 in 25 previously unsampled locations in one of the central Great Basin mountain ranges, to conduct a preliminary external evaluation of the models (Thomson et al. 2007), but we did not have sufficient data to explicitly test the transferability of indicator species.

The extent to which particular indicator species are transferable is relevant to the management of extensive areas, including those in which there may be geographic differentiation in the responses of widely distributed organisms to their environment. Therefore, in the current project, we sought to develop a transferable model for identifying sets of indicator species that explained considerable variation in species richness. In this project, we also compared predictions of species richness based on these indicator species to predictions based on a set of environmental variables. Our current project allowed us to conduct external evaluations of the spatial and temporal transferability of indicator species and environmental variables that were considerably more rigorous than our previous (Thomson et al. 2007) evaluations. In the current work, for example, we tested the extent to which indicator species identified from models built with data from the central Great Basin predicted variation in species richness of birds and butterflies in the zoogeographically distinct western Great Basin (Behle, 1963, 1978; Austin and Murphy 1987), and vice versa. In our current work, we also tested whether models built from data collected over one to three years in a given subregion explained variation in species richness in that same subregion during one to three years of later sampling.

Theory and practical application of occupancy models: hierarchical models of occupancy

Species richness traditionally has been measured as the number of species observed. However, species richness also can be represented as the aggregate probability of occurrence of many individual species. Relatively few studies have combined single-species occupancy models to estimate patterns of occupancy of multiple species and to relate these community- or assemblage-level patterns to environmental variables (but see Carillo-Rubio et al. 2014). In theory, multiple-species occupancy models (Royle and Dorazio 2008) eliminate the need to run many, potentially dozens, of single-species models. Hierarchical occupancy models are applicable to analysis of nested data (e.g., species occurrences nested within species richness of a community) (Gelman and Hill 2007) because they allow for modeling relations among levels in the hierarchy and variability in species richness at all levels. For example, a hierarchical model allows one to account for variation in detection probabilities among species when estimating credible intervals around species-richness metrics at the community level. Like all occupancy models, hierarchical models also allow one to differentiate the sampling process (detection) and the state process (occupancy of the community).

Hierarchical models assume that all species within a community are members of one multiple-species population. Therefore, these models allow one to obtain occupancy estimates for species with detection probabilities that are too low to enable single-species occupancy estimation. In these cases, species with relatively high detection probabilities inform occupancy estimates for those with relatively low detection probabilities (Dorazio et al. 2010). However, a relatively small number of species can disproportionately affect inferences about covariates' associations with species richness (Zipkin et al. 2009).

We used hierarchical models of occupancy to explore species richness of the community of breeding birds in the Chesapeake Bay Lowlands and the central and western Great Basin and abiotic and biotic environmental attributes associated with species richness. Because the biology and environmental associations of the species within each community are highly diverse, we grouped species into three guilds on the basis of nesting stratum: on the ground or in low shrubs, in tall shrubs or trees, or in tree cavities.

Theory and practical application of occupancy models: estimation of the occupancy of butterflies in diverse biogeographic regions

The population dynamics of individual species of butterflies have been examined via both mark-recapture analyses (e.g., Brown and Ehrlich 1980, Fleishman et al. 2002, Leidner and Haddad 2011) and occupancy models (e.g., Pellet 2008, van Strien et al. 2011, Bried et al. 2012, Roth et al. 2014). Collection of data on occupancy of many species within a butterfly assemblage, and therefore application of occupancy models to many species rather than to one or a small number of species, is complicated by many sources of variation in phenology (e.g., Baughman et al. 1988, Weiss et al. 1988). Moreover, the number of generations per year varies among and within species, and can be plastic. Accordingly, it is quite difficult to gauge, *a priori*, the period in which a given species is available for sampling.

Assemblage–level surveys of butterflies traditionally addressed variation in phenology by conducting surveys every one to three weeks across the assemblage’s flight season. This method maximizes the likelihood that at least one or two surveys will coincide with each species’ flight. However, one survey is insufficient to estimate detection probability, and over several weeks, butterfly assemblages are not closed. If the flight season of a species can be estimated, then multiple surveys potentially can be used to develop a detection history. But the occupancy status of sample units is not constant across the season, and changes in occupancy are not random. Therefore, detection estimates that treat multiple surveys as replicate samples of the same species may be negatively biased, and the resulting estimates of occupancy positively biased. Another possibility, not mutually exclusive, is to sample each site repeatedly on each sampling date (the robust design; Kendall *et al.*, 1997). A third option is to relax the closure assumption by assuming that species are available for sampling at different times (Kendall *et al.* 2013).

We explored the extent to which occupancy of butterflies in the Chesapeake Bay Lowlands, central Great Basin, and western Great Basin could be explained on the basis of vegetation, topography, and other environmental attributes. We included survey–specific covariates of detection probability, and we modeled occupancy and detection in multiple years as a function of the same covariates to examine the temporal transferability of results. We also examined whether results for species that occur in two of the assemblages were geographically consistent. Furthermore, we examined the degree to which assumptions of closure at the single-species level were met with an assemblage-level sampling design.

Theory and practical application of occupancy models: environmental associations with multiple states of anuran occupancy

The occupancy model of MacKenzie *et al.* (2002, 2006) does not address abundance at each sample unit. This limitation to understanding of the causes of spatial variation in the abundances of populations led to extensions of the model that accommodate data on the relative abundance and other attributes of species at sample units (Royle and Nichols 2003, Nichols *et al.* 2007, MacKenzie *et al.* 2009). One set of extensions was developed for data from surveys that record multiple states of occupancy (Nichols *et al.* 2007, MacKenzie *et al.* 2009), where states include abundance or density classes (MacKenzie *et al.* 2009, Veran *et al.* 2016). These models have been used to evaluate hypothesized associations between attributes of sample units and the relative abundances of populations that occupy the sample units. For example, Goswami *et al* (2014) recorded the density of elephant dung piles and tracks on sample units and used multiple-state occupancy models to evaluate the roles of protected areas and human presence on the intensity of land use by Asian elephants (*Elephas maximus*).

Concerns about declines in populations of amphibians in the 1980s and 1990s (Wake 1991) led to the development of several state and federal amphibian monitoring programs (e.g., the North American Amphibian Monitoring Program (Weir and Mossman 2005). In many of these programs, the calling intensity of breeding choruses at wetlands is recorded as an ordered categorical variable (Weir and Mossman 2005). The data from these surveys provide information not only on occupancy, but on relative abundance across sample units. We used similar field methods and data to identify attributes of wetlands and the surrounding terrestrial environment

that were associated with populations of high relative abundance. We compared those attributes to the attributes of wetlands occupied by amphibian populations of any abundance class.

Responses of songbird occupancy to environmental change

Increases in human population size and associated urbanization are a major source of land-cover fragmentation and contemporary environmental change. These changes can increase the amount and quality of habitat for some native species of animals, including white-tailed deer. The deer, in turn, have the potential to further change levels of land-cover fragmentation and vegetation structure by consuming herbaceous and woody vegetation. Populations of both native and non-native deer have increased in many locations worldwide, prompting studies of ecosystem responses to abundant deer in Europe and North America (Knox 1997, Côté et al. 2004).

Intensive browsing by deer can lead to simplification and reduction of biomass in understory vegetation (Fuller 2001, Stockton et al. 2005, Martin et al. 2010), especially when deer become less selective as their abundance increases (Augustine and McNaughton 1998). Such vegetation changes are believed to have prompted declines in foliage-dwelling invertebrates (Allombert et al. 2005). Vegetation volume affects the quality of habitat for many breeding songbird species (Mills et al. 1991). Therefore, high abundances of deer can change habitat structure and food availability for birds, especially those that are associated with lower forest strata.

In the eastern United States, the abundance of white-tailed deer has increased substantially over the past century (Côté et al. 2004). For example, between 1931 and early 1990, the deer population in Virginia was estimated to have grown 36-fold as predators were extirpated, large areas in which deer formerly were hunted became urbanized, and land use fragmented forest cover (McShea et al. 2003, Lovely et al. 2013). Fragmentation provides deer with ready access to abundant forage at sunlit edges between forest and roadsides, grasslands, agricultural fields, or residential neighborhoods, while providing cover in nearby forest (Augustine and de Calesta 2003, Lovely et al. 2013).

Several studies have suggested a link between deer browsing and songbird dynamics. Species richness and abundance declined as deer density increased in Pennsylvania (deCalesta 1994) and Massachusetts (DeGraaf et al. 1991). Islands in southern British Columbia with high densities of black-tailed deer (*Odocoileus hemionus*) had lower densities of Rufous Hummingbirds (*Selasphorus rufus*), Song Sparrows (*Melospiza melodia*), and Fox Sparrows (*Passerella iliaca*) than deer-free islands (Martin et al. 2011). Further north in British Columbia, on the Haida Gwaii archipelago, long-term declines in abundance and diversity of understory birds were connected to the depletion of understory vegetation by introduced black-tailed deer (Chollet et al. 2014). Following experimental deer exclosure in Virginia, abundance of ground-nesting and intermediate canopy-nesting birds increased as understory vegetation regenerated (McShea and Rappole 2000). In Britain, Eurasian Blackcaps (*Sylvia atricapilla*), which are associated with early successional forest, were more abundant, settled earlier each spring, and had better body condition in areas where roe deer (*Capreolus capreolus*) and introduced Reeves's muntjac (*Muntiacus reevesi*) were experimentally excluded (Holt et al. 2013). At the state and provincial levels, the abundance of deer was related to declines of understory-nesting and foraging birds (Chollet and Martin 2013).

These effects of deer on birds, primarily mediated by browsing on understory foliage, can be magnified in forest fragments if deer activity becomes concentrated in relatively small forest patches (Augustine and de Calesta 2003). Evidence of the effects of deer on songbirds primarily is derived from studies on isolated or small forested sites. Only two studies examined the effects of deer on avian communities at extents larger than forest patches, and we are not aware of any research that examined associations between deer and forest songbirds at a regional level with fine-grained estimates of the density of deer and birds. By quantifying deer pellet and songbird densities across a large region in coastal Virginia over four years, we tested whether densities of species that nest and forage in the lowest stratum of forest foliage (i.e., vegetation on the ground and in the understory) was negatively correlated with intensity of deer use. We also explored whether relations between deer and songbirds were consistent along a gradient of intensity of deer use. Our work allowed us to examine how songbird densities may change as the level of forest fragmentation and relative intensity of deer use changes.

Partitioning drivers of beta diversity

Understanding the causes of variation in species composition through space and time (i.e., beta diversity), and relative variation in species richness (alpha diversity) and composition, is highly relevant to management. However, variation in beta diversity is poorly understood. For example, differences in temporal variation in species composition might inform the duration of or the inferences derived from monitoring.

Beta diversity can be partitioned into two components, turnover and nestedness, which reflect different ecological processes (Baselga 2010) (Figure 2). Turnover in space or time occurs when a species that previously was present becomes absent, and a different species becomes present. Nestedness occurs when the species present in locations with relatively low species richness are statistical subsets of the species present in locations with relatively high species richness. Beta diversity can be partitioned additively into turnover and nestedness components, with the sum of turnover and nestedness equal to total beta diversity (Baselga 2010). Baselga (2010) defined the Sørensen dissimilarity index as total beta diversity, the Simpson dissimilarity index as beta diversity due to turnover, and the difference between these two indices as beta diversity due to nestedness.

Both turnover and nestedness can be defined spatially and temporally. Species composition can differ among locations within a region, resulting in high regional species richness even if individual locations are occupied by few species. Species composition can change at one location through time, resulting in high species richness over years or decades even if that location is occupied by few species over days or months and species richness at a given point in time is fairly consistent. Both spatial and temporal beta diversity contribute to species richness, but few studies have considered the relative contributions of each to local or regional species richness.

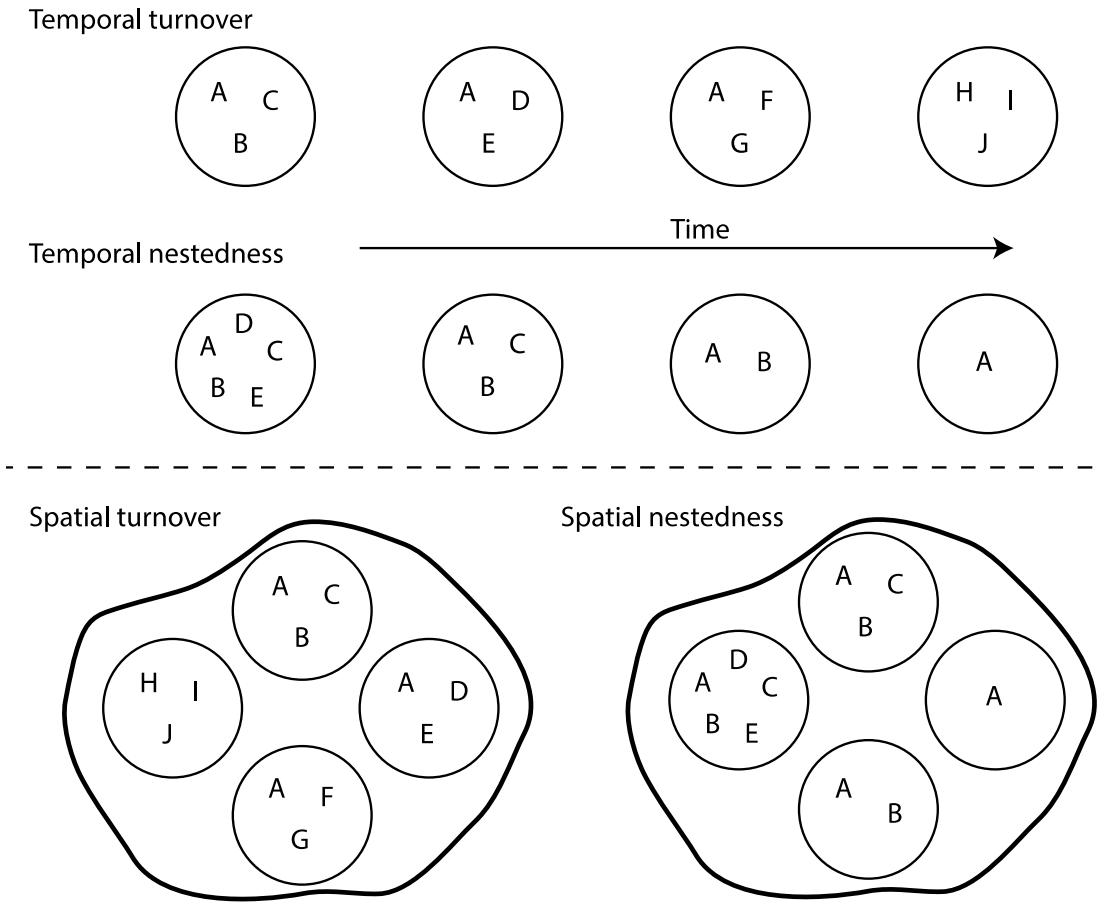


Figure 2. Examples of temporal and spatial turnover and nestedness. Different letters denote different species; small circles are points, transects, or canyons; and large bounding regions (thick black lines) are canyons or mountain ranges. Temporal turnover occurs when species' identities change through time. Temporal nestedness occurs when species are lost or gained through time. Spatial turnover and nestedness are defined similarly, but changes in species' identities or losses and gains of species occur through space rather than through time.

Comparisons of beta diversity among spatial resolutions can identify whether there are consistent patterns in species composition at any of them, which might provide insight into the natural and anthropogenic processes that affect the composition of a given assemblage. Such understanding can inform selection of spatial extents and resolutions for management, including monitoring. For example, high turnover of species among locations in a region might indicate that species can move easily among locations or have relatively plastic resource requirements. By contrast, low turnover of species among locations in a region might indicate an association of these species with fine-resolution environmental characteristics.

Although it is well established that sampling is affected by environmental conditions, and that local environmental heterogeneity (e.g., edges between land-cover types) may be associated with beta diversity, relatively little work has considered whether and how beta diversity changes along

environmental gradients. For example, it is unclear whether local climate, topography, or vegetation is associated consistently with temporal or spatial variation in faunal composition and, if so, at which spatial resolutions.

Understanding how species composition varies through space and time may be applicable to the management and monitoring of extensive areas. We analyzed spatial and temporal turnover and nestedness of bird and butterfly assemblages in the central and western Great Basin. We compared estimates of turnover and nestedness at two spatial resolutions (within canyons and among canyons) to determine whether assemblage composition was more consistent at either resolution. We are relating estimates of turnover and nestedness to environmental variables to evaluate whether these attributes are associated with beta diversity. We distinguish our analyses from others that assessed correlations between beta diversity and environmental diversity (e.g., Mantel tests) because the latter focused on variation in species composition rather than variation in beta diversity.

Materials and Methods

Field sampling

Study locations. Field sampling was integral to all of our project's objectives and tasks. We sampled anurans, birds, and butterflies in the Chesapeake Bay Lowlands. We sampled birds and butterflies in the central Great Basin and western Great Basin. We did not sample anurans in the Great Basin because few anurans occur in the region. More of our analyses and results focus on birds and butterflies than on anurans simply because anurans could not be sampled in all regions. However, all three taxonomic groups often are a focus of assessment, monitoring, and conservation planning and action. Therefore, our work not only informs methods for evaluating the status and potential effects of land use on these diverse groups, but may be directly applicable to efforts to maintain them.

In the Chesapeake Bay Lowlands, our study area included the Virginia Peninsula between Toano and Hampton (Charles, City, Henrico, James City, Newport News, Williamsburg, and York Counties, Virginia) and the Middle Peninsula near West Point (King and Queen and King William Counties, Virginia) (Figure 3). The Virginia Peninsula includes of a network of natural wetlands and ponds and anthropogenic ponds that are embedded in a matrix of remnant upland and bottomland hardwood forest, agricultural areas, and areas of low- to high-density housing. Our sampling included Joint Base Langley–Eustis. We focused on Joint Base Langley–Eustis because it was the most accessible installation in the Chesapeake Bay Lowlands. We conducted field sampling with the area recognized as Fort Eustis prior to its consolidation with Langley Air Force Base in 2010. The primary mission of Fort Eustis is Army transportation training, research and development, engineering, and operations, including aviation and marine shipping activities. Access to other installations in the Chesapeake Bay Lowlands, including Camp Peary and Naval Weapons Station Yorktown / Cheatham Annex, is restricted. We requested but were denied access to Fort A.P. Hill.

Depending on hydrology and soil drainage, canopy trees in deciduous forest in the Chesapeake Bay Lowlands may include red maple (*Acer rubrum*), birch (*Betula* spp.), black walnut (*Juglans nigra*), sweetgum (*Liquidambar styraciflua*), tulip popular (*Liriodendron tulipifera*), water or black tupelo (*Nyssa aquatica*, *N. sylvatica*), sycamore (*Platanus occidentalis*), and oaks (*Quercus* spp.) (Weakly 2012). The canopy of upland coniferous forests is dominated by loblolly pine (*Pinus taeda*). Sweetgum also is a dominant species in early successional stands (Monette and Ware 1983, Weakly 2012). The canopy of upland deciduous forest is dominated by American beech (*Fagus grandifolia*), oaks, and American holly (*Ilex opaca*). Loblolly pine, tulip popular, and sweetgum also are present (Monette and Ware 1983, Weakly 2012).

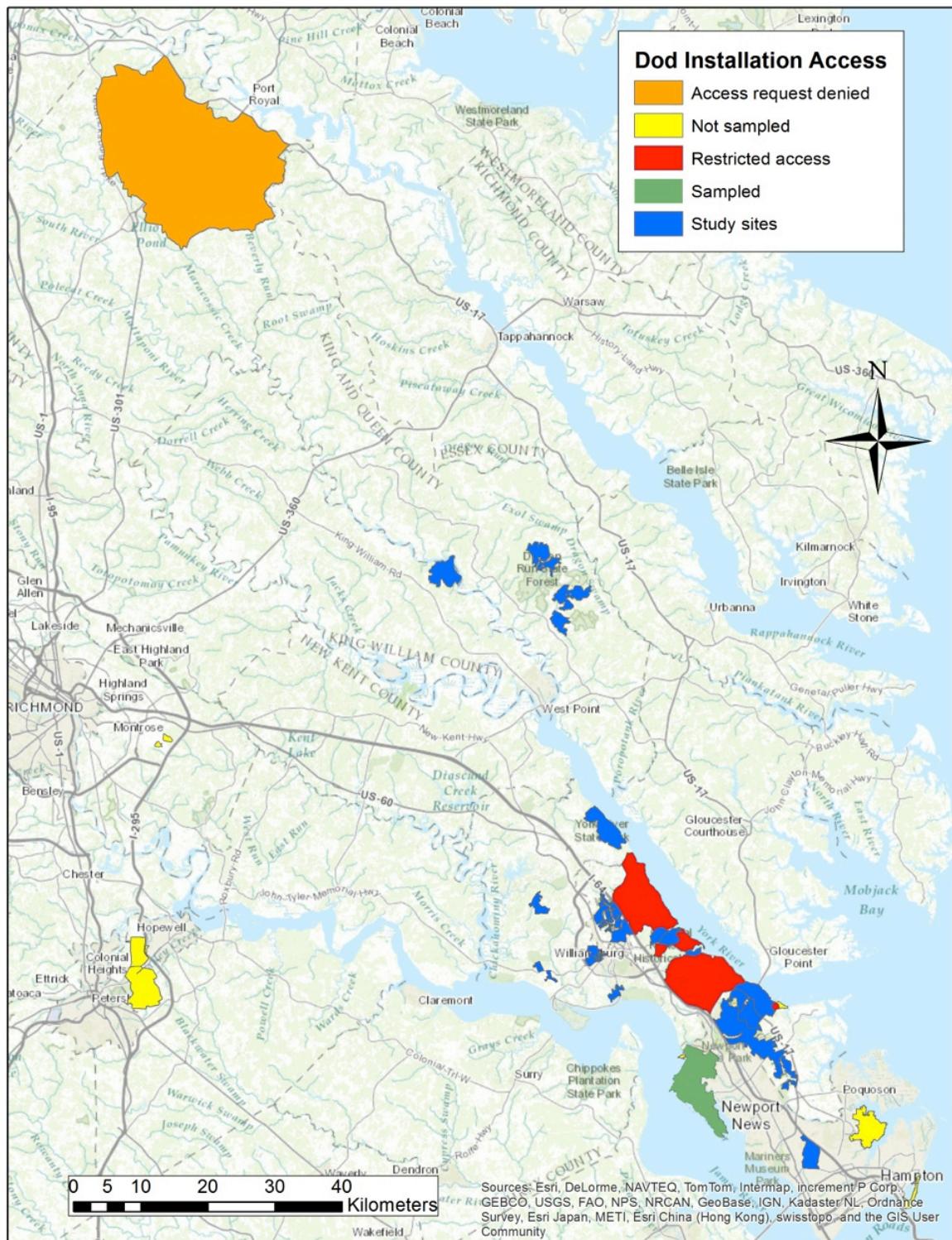


Figure 3. Department of Defense Installations within the Chesapeake Bay Lowlands and locations of other areas in which we sampled anurans, birds, and butterflies.

Behle (1963) recognized five centers of differentiation for birds in the Great Basin (Warner, Sierra Nevada, western Great Basin, eastern Great Basin, Inyo). He defined a center of differentiation as an expression of the concept that “the area so designated contains several geographic races representing different species and genera, that the ranges of the several kinds coincide rather closely, and that the characters of each kind are best developed in the particular region. These features imply that the different races have originated in the area either because of the modifying influence of some environmental factor or factors that have had an effect on the several forms, or a barrier of some sort has delimited the several kinds so that they show a common distributional pattern” (page 1168). Similarly, Austin and Murphy (1987) recognized six centers of differentiation for butterflies in the Great Basin (Warner, Jarbidge, Central, Toiyabe, Snake, and Inyo). Our study locations in the central Great Basin are within the eastern (Behle 1963) or Toiyabe (Austin and Murphy 1987) center of differentiation, and those in the western Great Basin fall within the Inyo center of differentiation. Exploring similarities and differences in ecological patterns between centers of differentiation is relevant because the management plans of public departments and agencies sometimes assume that a single management prescription will be effective across the entire Great Basin. However, few studies have addressed whether relations between species richness and environmental variables, or between individual species and environmental variables, are consistent among these centers.

Our central Great Basin study area included much of the adjacent Shoshone Mountains and Toiyabe, Toquima, and Monitor Ranges (Lander, Nye, and Eureka Counties, Nevada). In the western Great Basin, our study area included part of the east slope of the Sierra Nevada and the adjacent Wassuk Range and Sweetwater Mountains (Mono County, California and Mineral, Douglas, and Lyon Counties, Nevada). Our study area also encompassed parts of the Hawthorne Army Depot and Marine Corps Mountain Warfare Training Center (Figure 4). Hawthorne Army Depot stores conventional munitions, demilitarizes and disposes of unserviceable, obsolete, and surplus munitions; and maintains serviceability through inspection and renovation to ensure munitions readiness. Although most of the installation is flat, at relatively low elevation, and sparsely vegetated, it also includes Mt. Grant, which is the highest (3440 m) peak in the Wassuk Range and Mineral County, Nevada. In part because access to Mt. Grant long has been restricted, and became highly restricted in 2001, land use is limited and habitat quality for many taxonomic groups, including birds and butterflies, is high. The Marine Corps Mountain Warfare Training Center emphasizes training of combat forces to operate at high elevations, in complex terrain, and in cold weather. Most training occurs on US Forest Service lands under a special use permit. Other DoD installations in the Great Basin, such as Naval Air Station Fallon, Hill Air Force Range, Wendover Range, Deseret Test Center, and Dugway Proving Ground, are at relatively low elevations, are sparsely vegetated, and are inhabited by relatively few species of songbirds and butterflies. Nellis Air Force Base largely is located within the Mojave Desert rather than the Great Basin. We requested but were denied access to the Tonopah Test Range.

Among the dominant land-cover types in the central and western Great Basin are woodlands dominated by single-leaf pinyon (*Pinus monophylla*) and juniper (*Juniperus osteosperma*, *J. occidentalis*), shrubsteppe dominated by sagebrush (*Artemisia* spp.), and riparian woodlands dominated by deciduous trees (e.g., aspen [*Populus tremuloides*], chokecherry [*Prunus virginiana*]) and shrubs (e.g., willow [*Salix* spp.], Woods' rose [*Rosa woodsii*]). Jeffrey pine

(*Pinus jeffreyi*), lodgepole pine (*Pinus contorta*), and red fir (*Abies magnifica*) also are dominant trees in some parts of the east slope of the Sierra Nevada and Wassuk Range.

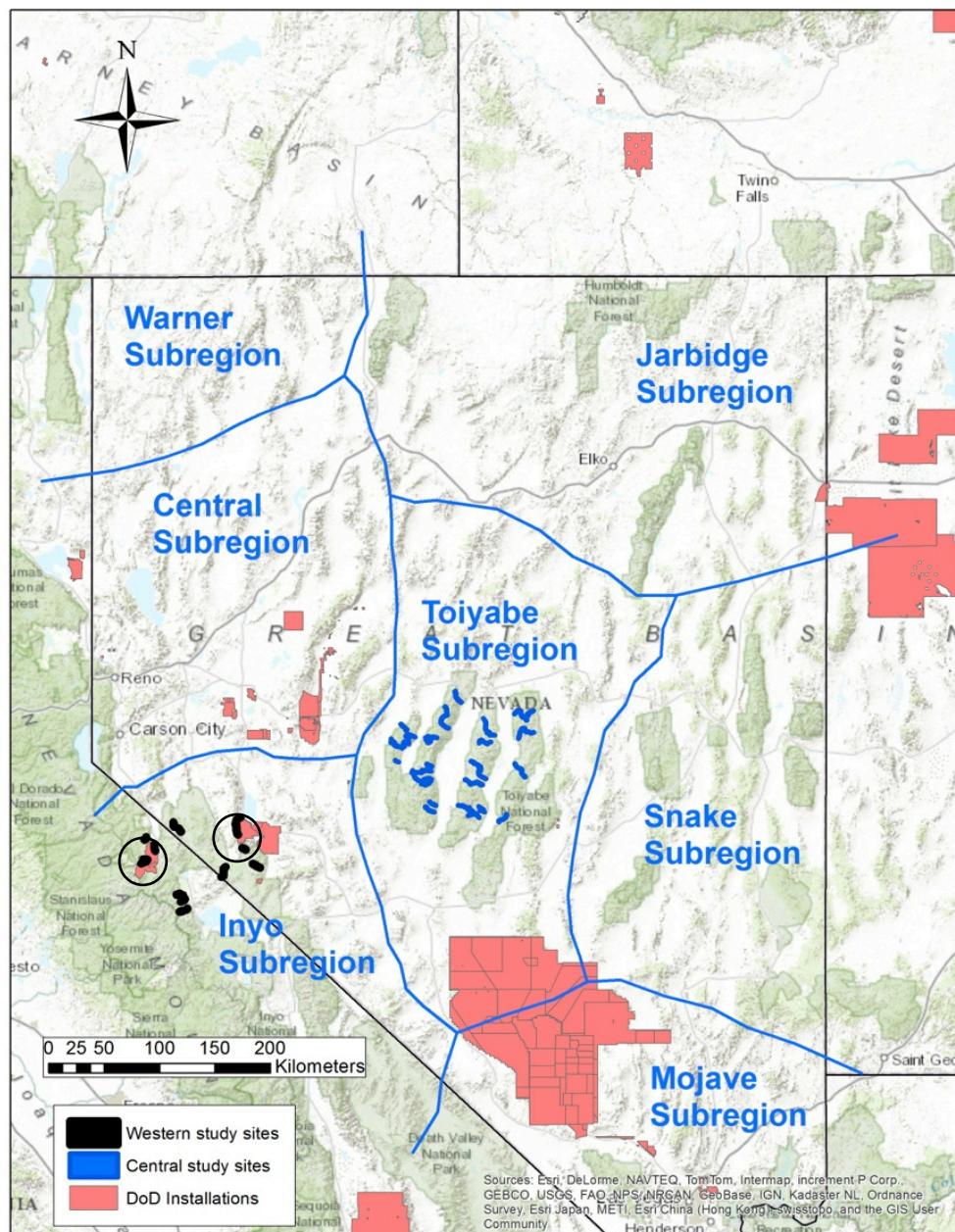


Figure 4. Centers of faunal differentiation with the Great Basin (Austin and Murphy 1987), locations of our study sites within the Inyo Subregion (western Great Basin) and Toiyabe Subregion (central Great Basin), and locations of most DoD installations in the Great Basin. Open black circles indicate the locations of the Marine Corps Mountain Warfare Training Center (left) and Mt. Grant (right).

Anurans. We delineated an anuran study area of 3768 km² that included the Virginia Peninsula and portions of the Richmond municipal area. This area was bounded by the Chesapeake Bay to the east, York River to the north, and James River to the south. Approximately 3.4% of the study area was covered by wetlands; freshwater emergent wetlands covered 1.9% (US Fish and Wildlife Service 2010). Fifty-four percent of the study area was classified as forest (SE GAP 2010). Developed areas and agriculture covered 24.0% and 12.1% of the study area, respectively. We stratified the study area with the smallest US Geological Survey Hydrological Unit Classification (HUC 12) (Seaber et al. 1987) and 2000 census data (US Census Bureau 2010). We assigned each HUC to one of four housing-density strata (Radeloff et al. 2005): very low (≥ 0 and < 6.18 houses/km²), low (≥ 6.18 and < 49.42), medium (≥ 49.42 and < 741.32), and high (≥ 741.32). We created a sampling frame of wetlands and ponds (hereafter, wetlands) by combining data from the National Wetlands Inventory (US Fish and Wildlife Service 2010) with data on a set of wetlands that we had identified. Prior to the field season in 2011, we used aerial imagery from the 2009 Virginia Base Mapping Program (Virginia Information Technologies Agency 2009) to hand-digitize wetlands not captured by the National Wetlands Inventory in a Geographic Information System (GIS) (ArcMap 9.0, ESRI 2009). From the sampling frame, we randomly selected wetlands from each of the housing-density strata; selected wetlands were ≥ 1 km apart. The accessibility of the wetlands was evaluated prior to the field season. If a given wetland was not accessible (e.g., unsafe to access or on private property with restricted access), we randomly selected another wetland. The mean distance between neighboring wetlands in the final sample was 2.63 km (standard deviation [SD] 1.43).

Our sampling protocol for anurans was based on the North American Amphibian Monitoring Protocol (Weir and Mossman 2005). We conducted surveys from February through July to capture the three periods during which different species breed (Garrett 2002). Each survey focused on the peak month of vocalization for a breeding period (mid February through mid March, mid April through mid May, and mid June through mid July). We adjusted the start date of each survey on the basis of annual spring temperatures and precipitation. We sampled adjacent to a pond or wetland. We sampled each pond three times during each breeding period, for a total of nine visits per pond per year. Three visits per breeding season is standard for anuran surveys (Weir et al. 2005, 2009). Visits began 30 min after sunset and continued until 0100 (Bowers et al. 1998, Bridges and Dorcas 2000). We noted the time that each visit began. During each visit, we noted time of first detection for all species calling within 5 min [detection probabilities increase slightly as duration of sampling increases (Dorcas et al. 2009)], estimated abundance of males categorically (1, individuals can be counted; 2, calls of individuals can be distinguished but there is some overlap of calls; 3, full chorus with calls that are constant, continuous, and overlapping), and estimated covariates known to affect detection of anurans (e.g., ambient sound, temperature, wind speed).

At the time of each survey, which we recorded, we measured ambient temperature (°C) and wind speed (m sec⁻¹) with a hand-held weather station (Kestrel 2000, Nielsen-Kellerman Co., Boothwyn, Pennsylvania) and wind speed in the canopy according to the Beaufort scale (see www.spc.noaa.gov/faq/tornado/beaufort.html). We also recorded traffic volumes during the count, which affect ambient sound levels and detection probabilities (0, none; 1, 1 car passing; 2, 2–5 cars passing; 3, continuous traffic passing [about 6–10 cars]; 4, continuous traffic passing, with construction or industrial sounds). We did not conduct surveys if wind speed exceeded 3 on

the Beaufort scale (leaves and small twigs constantly moving, light flags extended), during snow, during rainfall of sufficient intensity to affect hearing ability, or if temperatures were before the threshold defined by the North American Amphibian Monitoring Protocol (5.6° during the first breeding period, 12.8° during the second breeding period, and 18.3° during the third breeding period).

Anuran data were included in analyses of periodicity of sampling (trade-offs between single-day and multiple-days sampling) and of environmental associations with multiple states of occupancy.

Birds. To survey birds in the Chesapeake Bay Lowlands and central and western Great Basin, we conducted point counts (*counts*) during the breeding season (late May through June) (Dobkin and Rich 1998). Despite differences in elevation and latitude, the timing of the breeding season is similar among locations and years. The sampling period overlaps among ecosystems in part because of the protracted songbird migration in the eastern United States. The peak of the migration period in the eastern United States varies among years but generally occurs during the first two weeks of May. We did not survey birds in the Chesapeake Bay Lowlands until most species that breed further north had passed through the area. Similarly, birds that breed in the Great Basin are present in that region earlier in May, but the ratio of birds that breed in the Great Basin to birds that breed further north increases throughout the month.

Most point centers were > 350 m apart, which minimized the probability that observer activity would cause individuals to move among points. During each visit, we recorded by sound or sight all birds using terrestrial habitat within the point. We visited each point three times per year for 8 min per count (Buckland et al. 2001, Siegel et al. 2001, Dickson et al. 2009). We recorded whether a detection occurred during the first 5 min or the last 3 min. In each of our ecosystems, observers used a laser rangefinder to estimate the distance to each bird detected. In the Chesapeake Bay Lowlands, we estimated distance as a continuous variable. In the Great Basin, we sampled birds with fixed-radius point counts, and used distance bins: ≤10 m, >10–25 m, >25–50 m, >50–75 m, >75–100 m, and > 100 m. The distance bins and distance thresholds we used followed standard protocols outlined by Ralph et al. (1993, 1995) and reiterated by Matsuoka et al. (2014). In our analyses, we included detections within 100 m of the observer, but generally did not differentiate distances within that radius. We maintained and archived records of birds detected at distances of >100 m.

At the time of each count in the Chesapeake Bay Lowlands (we recorded the time), we recorded ambient temperature (°C) and wind speed (m sec⁻¹) with a hand-held weather station (Kestrel 2000, Nielsen-Kellerman Co., Boothwyn, Pennsylvania) and wind speed in the canopy according to the Beaufort scale. We also recorded traffic volumes during the count, which affect ambient sound levels and detection probabilities (0, none; 1, 1 car passing; 2, 2–5 cars passing; 3, continuous traffic passing [about 6–10 cars]; 4, continuous traffic passing, with construction or industrial sounds).

In the Chesapeake Bay Lowlands, we established points within riparian forests and upland coniferous and deciduous forests. In the central and western Great Basin, points were positioned to sample the dominant land-cover types throughout the canyons.

The common names of birds that occur in the United States are standardized by the North American Classification Committee, an official committee of the American Ornithological Society. Our use of common and scientific names of birds follows the *Birds of North and Middle America Checklist*, the official source on the taxonomy of birds in North and Middle America, including adjacent islands.

Bird data from the Chesapeake Bay Lowlands were included in analyses of periodicity of sampling (duration of point counts), hierarchical occupancy, and responses of songbird occupancy to environmental change.

Bird data from the central and western Great Basin were included in analyses of hierarchical species richness, periodicity of sampling (duration of point counts and trade-offs between single-day and multiple-days sampling), estimation of species richness of multiple taxonomic groups on the basis of a single group, hierarchical occupancy, and drivers of beta diversity.

Butterflies. We sampled butterflies along transects, all of which encompassed points at which we surveyed birds. Because timing and duration of flight varies among butterfly species, locations, and years (Scott 1986), we sampled each transect approximately every two weeks throughout the majority of the flight season (late May through mid August). During every visit, we walked the length of each transect at a near-constant pace and recorded all butterfly species detected (Pollard and Yates 1993). Walking along transects is a standard method for surveying butterfly assemblages (Pollard and Yates 1993, Pullin 1995). Species that cannot be identified on the wing are captured and either identified in the hand or collected for identification in the laboratory.

In the Chesapeake Bay Lowlands, we sampled butterflies along a 0.5 km transect within each bird point. In the central Great Basin, we divided each canyon into 100-m vertical elevation bands from its mouth to its crest. In the western Great Basin, transects for butterflies covered the length of each canyon and were centered on bird points. We estimated abundance of each species along each transect. During each visit, we recorded the relative abundance (none, low, moderate, high) of individual plants (primarily forbs) from which one or more species of butterflies in those ecosystems are known to take nectar and, in the Great Basin, the relative abundance of sources of mud, such as stream crossings (none, low, moderate, high). Female fecundity in some species is related to nectar volume (Boggs and Ross 1993), and many species feed on dissolved minerals in moist soil (Scudder 1889, Arms et al. 1974).

Nomenclature for butterflies in the Chesapeake Bay Lowlands follows Pelham 2016.

Nomenclature for butterflies in the Great Basin follows Fleishman et al. 1997 and Austin 1998.

Butterfly data from the Chesapeake Bay Lowlands were included in analyses of the occupancy of butterflies in diverse biogeographic regions. Butterfly data from the central and western Great Basin were included in analyses of hierarchical species richness, periodicity of sampling (trade-offs between single-day and multiple-days sampling), estimation of species richness of multiple taxonomic groups on the basis of a single group, occupancy of butterflies in diverse biogeographic regions, and drivers of beta diversity.

Vegetation and other environmental covariates. To characterize vegetation composition and structure at each pond where we sampled anurans, we established three 1 x 3 m sampling plots along the edge of the pond (Figure 5). One plot was positioned at the location at which anurans were sampled. The other two plots were positioned at 20 m on either side of the anuran-sampling location. In each plot we measured water pH and water depth at 1 m from the edge of the pond. We measured composition and structure of aquatic and terrestrial vegetation in three adjacent 1-m² quadrats. One quadrat overlapped the water-land edge, one extended into the water, and one extended onto the land. In each plot we measured the percentage of cover of trees > 3 m, shrubs of different heights (> 0.5–3 m, > 0.3–0.5 m, 0.1–0.3 m, and < 0.1 m), grasses, forbs, moss and lichens, floating vegetation, emergent vegetation, and submerged vegetation (Mazerolle et al. 2005). We estimated the number of days without precipitation and the number of days since above-average precipitation (average within each of the three breeding periods) on the basis of records from the nearest airport. We also calculated the number of minutes between sunset and initiation of the survey and the Julian date (standardized to the first day of the survey).

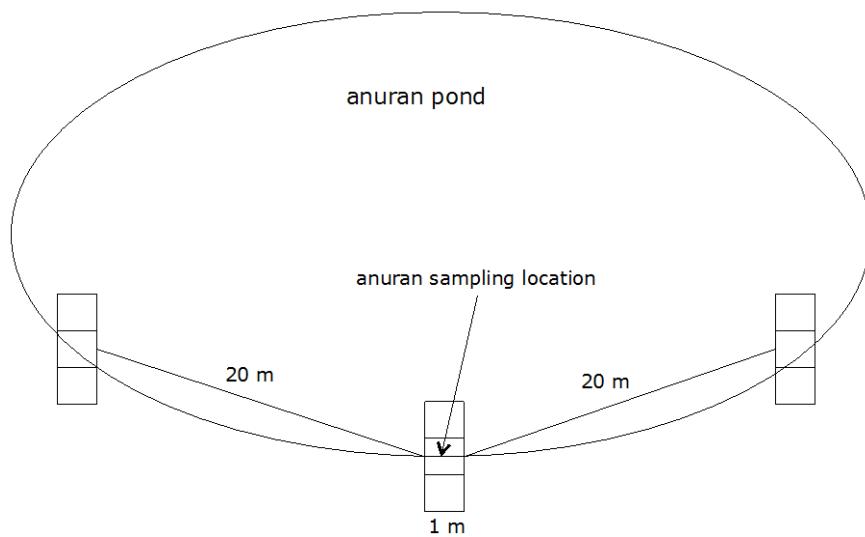


Figure 5. Design of vegetation sampling for anurans. Figure not to scale.

Data on vegetation and other environmental covariates associated with anurans were incorporated into analyses of environmental associations with multiple states of occupancy.

Methods for sampling local vegetation composition and structure at bird-survey points differed between the Chesapeake Bay Lowlands and the Great Basin (we used the same methods in the central and western Great Basin). The differences in part reflected that the diversity and, in most cases, the complexity of vegetation in the Chesapeake Bay Lowlands was greater than in the Great Basin. Also, our methods for the Great Basin were consistent with the methods we used during previous research on breeding birds in the region, which allowed us to augment the data collected for this project. Although field methods differed, the fundamental information captured in both regions was similar, facilitating inclusion of similar covariates in models and comparison of model outputs among regions.

To characterize local vegetation composition and structure at the bird-survey points in the Chesapeake Bay Lowlands, we measured four radial 15-m lines, oriented in each of the cardinal directions, from the center of the point (Figure 6). At each 1 m, we recorded the identity of all plants that touched each 10-cm vertical increment of a 1-m tall pole, and the highest point on the pole at which each plant touched. We recorded the species (if possible) or the functional group of all saplings ≤ 1 cm diameter and the presence of shrubs, non-native Japanese stiltgrass (*Microstegium vimineum*), other grasses, and forbs. We also recorded whether woody debris > 5 cm diameter, leaf litter, water, or bare ground intersected the pole on the ground. We used a moosehorn to determine whether canopy cover at each 1 m was nonzero.

We recorded each tree (1–10 cm diameter) within each quadrant (northeast, southeast, southwest, northwest) of a circle with 7.5-m radius extending from the center of the point. Within a circle with 15-m radius extending from the center of the point, we also recorded the genus, diameter at breast height (dbh), and stratum (canopy or subcanopy) of all live trees and snags > 10 cm dbh. Within the latter circle, we measured the dbh (if upright) and length of all downed wood > 10 cm dbh. Limbs of branched trees were measured separately, and only the portion of the wood within the circle was measured. To measure understory cover, we counted the number of decimeter segments of a 3-m tall pole that were $\geq 75\%$ visible when the pole was placed 15 m from the center of the point in each of the cardinal directions.

Vegetation data associated with birds in this region were included in analyses of hierarchical occupancy and responses of songbird occupancy to environmental change.

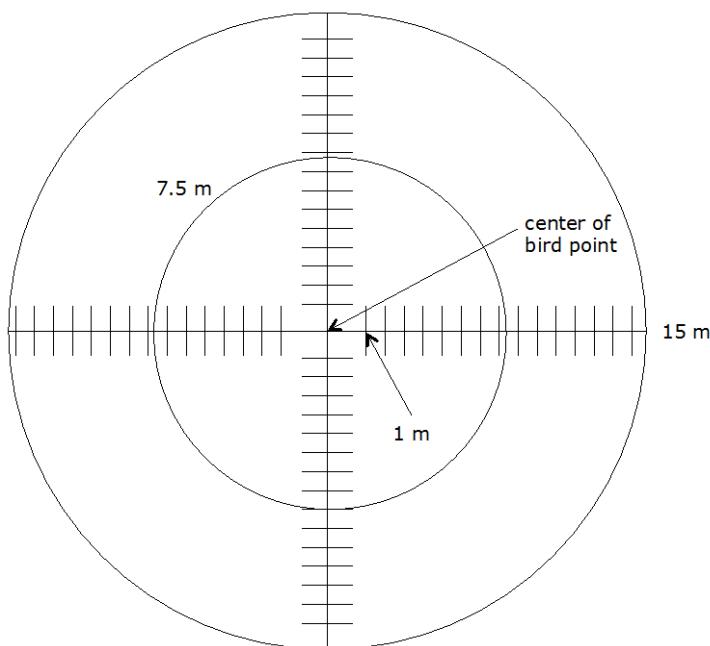


Figure 6. Design of vegetation sampling for birds in the Chesapeake Bay Lowlands.

To characterize local vegetation composition and structure at the bird-survey points in the central and western Great Basin, we measured three radial 30-m lines from the center of the point (Figure 7). Lines were separated from each other by 120 degrees. The distal end of each line became the center of a circular vegetation sampling unit with 11.3-m radius (0.04 ha). Within each unit, we recorded identities and sizes of all live trees (either dbh or basal diameter, depending on plant morphology). We recorded the identities and sizes of standing dead trees. We used a concave spherical densiometer to estimate proportion of canopy cover. To estimate frequency of shrubs and ground vegetation, we used an ocular tube with measurements taken at a 45-degree angle downward from the line of sight (Noon 1981). We recorded occurrence of dominant tree, shrub, and herbaceous taxa (approximately 20–30). We collected 21 densiometer and ocular tube readings at each plot: one each at 8 m, 16 m, and 24 m along the 30-m line from the center of the plot to the perimeter of each circle, and one while facing in each of the four cardinal directions from the center of each circle. Data on vegetation and other covariates associated with birds in the central and western Great Basin were included in analyses of hierarchical species richness, estimation of species richness of multiple taxonomic groups on the basis of a single group, and partitioning drivers of beta diversity.

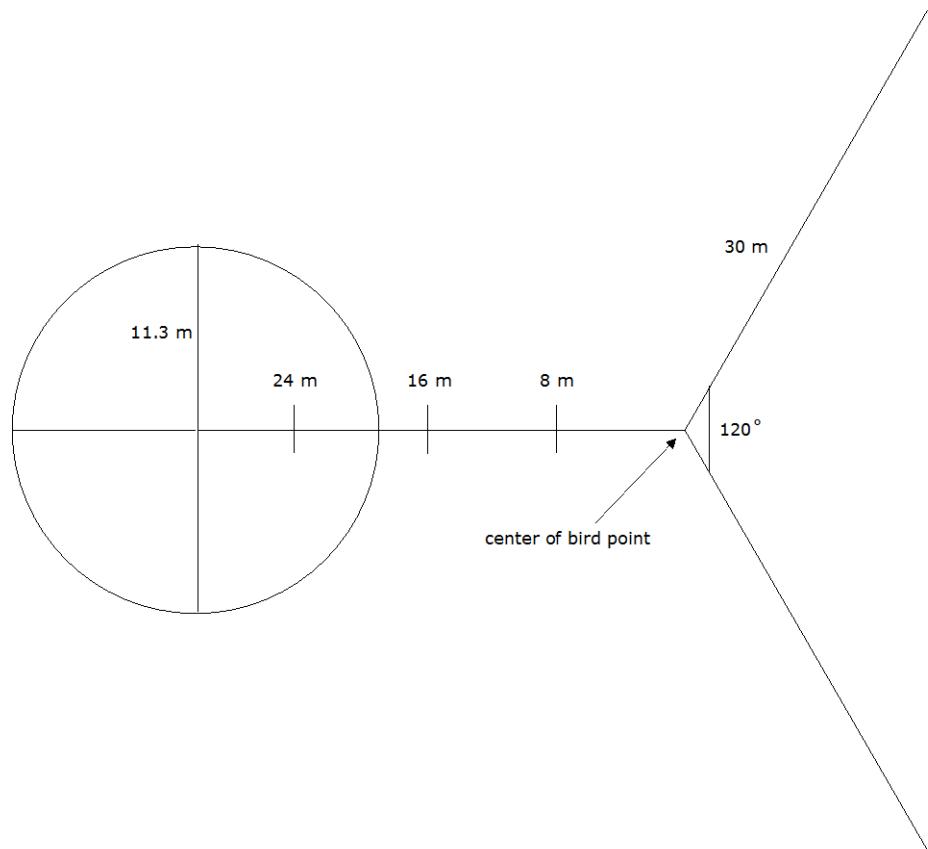


Figure 7. Design of vegetation sampling for birds in the central and western Great Basin.

As covariates in analyses of butterflies in the Chesapeake Bay Lowlands, we measured the length (km) of all edges between forest and agriculture, ruderal, or herbaceous-developed land cover; structural heterogeneity of the understory from 0–3 m above ground (the approximate

height of the white-tailed deer browse line [Allombert et al. 2005, Bressette et al. 2012]); the proportion of the basal area of trees (≥ 10 cm dbh) that was deciduous; the number of deciduous stems (single- or multiple-stemmed trees or shrubs; 1 to <10 cm dbh) below the canopy; and the categorical abundance of nectar. We included categorical abundance of nectar as a detection covariate. To derive edge length, we first obtained data on land cover at 30-m resolution (2013 Existing Vegetation Type data; www.landfire.gov). Next, we delineated edges between land-cover types in Geospatial Modeling Environment (www.spatialecology.com/gme/index.htm). We then derived edge length in ArcGIS 10.1 (ESRI, Redlands, California) as the mean of the 30-m cells within a 90-m buffer on either side of the transect. We used light detection and ranging (lidar) data that were captured from 22 April – 10 May 2010 and 21–31 March 2013 to estimate structural heterogeneity of the understory on the basis of density of returns at 10-m resolution, averaged among the 10-m cells within the 90-m buffer. We measured the proportion of basal area of trees that was deciduous within three circular plots (15-m radius) that were randomly placed within the 90-m buffer. We counted the number of deciduous stems within three circular plots (7.5-m radius), each of which was embedded within one of the 15-m plots. Covariates associated with butterflies in the Chesapeake Bay Lowlands were included in analyses of occupancy of butterflies.

As covariates in analyses of butterflies in the Great Basin, we included elevation, the square of elevation, terrain roughness, precipitation in the water year (1 October – 30 September) of sampling, and categorical abundance of nectar and mud as covariates of occupancy in the Great Basin. All reasonably might be expected to affect habitat quality for many butterfly species (e.g., Fleishman et al. 2001a, b). We included categorical abundance of nectar and mud as detection covariates. We derived mean elevation of the transect from a 10-m digital elevation model (www.ned.usgs.gov), assuming that the sampled area included 25 m on either side of the transect. We used a digital elevation model to derive terrain ruggedness (Riley et al. 1999) within 30-m circular neighborhoods and then averaged terrain ruggedness for the transect. We derived precipitation at 4-km resolution from the Parameter–elevation Relationships on Independent Slopes Model (PRISM). Covariates associated with butterflies in the central and western Great Basin were included in analyses of hierarchical species richness, periodicity of sampling (trade-offs between single-day and multiple-days sampling), estimation of species richness of multiple taxonomic groups on the basis of a single group, occupancy of butterflies in diverse biogeographic regions, and partitioning drivers of beta diversity.

Response of songbird occupancy to environmental change. We measured deer use and densities of forest songbirds in two areas of Virginia. Our primary study region, coastal Virginia, included the Virginia and Middle Peninsula on the coastal plain of southeastern Virginia from Newport News to West Point. In this area, we established 92 points in that we visited three times annually from 2010–2013. We randomly placed these points in wooded areas that we stratified on the basis of land ownership (private, city, county, state, and federal). Deer appeared to be highly abundant in coastal Virginia. Our second study region, inland Virginia, was approximately 200 km west of the coastal Virginia region, and encompassed the Shenandoah River Valley from Stuarts Draft to Harrisonburg. In this area, we established 99 points that we surveyed three times in 2012. We selected sites opportunistically on the basis of access, with the goal of even spatial representation. Deer appeared to be considerably less abundant than in coastal Virginia.

We used distance sampling to quantify deer pellets and forest songbirds. We surveyed birds with 8-min variable-distance point counts. Following each avian survey, we counted deer fecal pellets along two 60-m transects randomly placed within 150 m of the point (coastal Virginia) or centered on the point (inland Virginia). We assumed that pellet density reflected the relative intensity of deer use. Following McShea and Rappole (2000), we used Partners in Flight Species Assessment Database scores for bird conservation region 27 (Southeastern Coastal Plain) as a measure of conservation priority (Partners in Flight Science Committee 2012). We used the regional combined score for the breeding season, which incorporates the species' breeding distribution, population size, regional population trend, relative breeding density, and regional threats to reproduction. Higher scores indicate higher conservation priority.

Analytical methods

Hierarchical estimates of species richness

These data are hierarchically structured: points at which birds were surveyed, or transects at which butterflies were surveyed, are nested within canyons (which in turn are nested within mountain ranges) in both the central and western Great Basin. Our response variable was cumulative species richness across all years in which the location was surveyed. We modeled two levels of the data: points or transects and canyons. We treated canyon as a random effect, and used number of survey years as a control variable. We also estimated values of both point-level covariates and canyon-level covariates, reflecting our hypothesis that species richness may respond to phenomena that are relevant at different spatial resolutions. We ensured that highly collinear covariates were not included in the same analyses.

In the formulae below, i indexes point and j indexes canyon. x_i references point-level covariate i , whereas μ_j references canyon-level covariate j . In general, when we treated canyon as an indicator variable, we could apply three types of linear regression models:

- Constant slopes and intercept: $y = \alpha + \sum \beta_i x_i$
- Constant slopes, varying intercepts: $y = \alpha_j + \sum \beta_i x_i$
- Varying slopes and intercepts: $y = \alpha_{j[i]} + \sum \beta_{j[i]} x_i$

We first explored an unconditional means model, which does not include covariates. In this model, a different intercept (random effect) is fit for each canyon. This hierarchical model is fit to estimate components of variance across the two levels (canyons and points). The model is

$\rho = \frac{\tau^2}{\tau^2 + \sigma^2}$, where τ^2 is variance among the random intercepts (i.e., mean among-canyon variance), and σ^2 is residual variance (i.e., mean variability within canyons). We used the estimates of τ^2 and σ^2 to compute the intraclass correlation coefficient, ρ , which ranges from 0 (no variance among canyons) to 1 (no within-canyon variance).

Second, we fit two models that included point-level covariates only. The first of these, a standard multiple-regression model with fixed effects, had constant slopes and intercept (α). We pooled data across canyons. The model is $S_i = \alpha + \sum_i \beta_i x_i + \varepsilon_i$. The second of these models has constant

slope but random or varying intercept, which reflects the possibility that relations between cumulative species richness and point-level covariates vary among canyons. We treated the intercept as a random effect, thereby assuming that the intercept terms had a normal distribution. This model is

$$S_i = \alpha_{j[i]} + \sum_i \beta_i x_i + \varepsilon_i$$

$$\alpha_j \sim N(\mu_\alpha, \sigma_\alpha^2)$$

Third, we fit two models that included canyon-level covariates. The first of these had constant slopes and a random intercept. The intercept could be a function of the canyon-level covariates, u_j . This model is

$$S_i = \alpha_{j[i]} + \sum_i \beta_i x_i + \varepsilon_i$$

$$\alpha_j = a + b u_j + \eta_j$$

The second of the models that included canyon-level covariates had random slopes and a random intercept. Both the slopes and the intercept could vary among canyons, as a function of the canyon-level covariates. This model is

$$S_i = \alpha_{j[i]} + \sum_i \beta_{j[i]} x_i + \varepsilon_i$$

$$\alpha_j = a_o + b_o u_j + \eta_{j1}$$

$$\beta_j = a_1 + b_1 u_j + \eta_{j2}$$

Periodicity of sampling: duration of point counts of birds

To estimate detection probabilities (the probability of detecting a species at a site if it is present) (p) and occupancy (the probability that a given location is occupied by a species) (ψ) of breeding birds in the Chesapeake Bay Lowlands and central and western Great Basin, we used a hierarchical, single-season (single-year) occupancy model (MacKenzie et al. 2006). We modified the general form of the model to allow detection probability to vary among observers (Diefenbach et al. 2003, Alldredge et al. 2007).

We modeled single-season occupancy (MacKenzie et al. 2002) in 2012 and 2013 for species detected during 5-min counts (i.e., 8-min counts truncated at 5 min) and species detected during 8-min counts. We estimated occupancy for all species with a detection probability ≥ 0.3 in both 5-min and 8-min counts in a given year and for which the confidence intervals around the detection probability did not range from zero to one. We tested whether the occupancy estimates for each species were significantly different (the 95% confidence interval centered on the difference between the 5-min and 8-min occupancy estimate did not include zero [Schenker and

Gentleman 2001]) when based on 5-min versus 8-min counts. We report the percentage (mean \pm SE) of species for which occupancy models converged and produced estimates (i.e., 95% confidence interval did not range from zero to one and other diagnostics did not indicate estimation problems), and for which detection probabilities based on both count durations were ≥ 0.3 .

To examine whether inferences about occupancy over two years were consistent over longer periods of time, we also fit single-season occupancy models to data from 2009–2013 on American Robins (*Turdus migratorius*), MacGillivray's Warblers (*Geothlypis tolmiei*), and Vesper Sparrows (*Pooecetes gramineus*) in the central Great Basin. These species collectively span gradients of land-cover associations, local rarity, and ease of identification. We examined difference in the precision of occupancy estimates based on 5-min and 8-min counts. We defined precision as the coefficient of variation (CV). We conducted all analyses in package Unmarked (Fiske et al. 2015) in R (R Core Team 2014).

Periodicity of sampling: trade-offs between single-day and multiple-days sampling

We fit separate models of occupancy and detection (MacKenzie et al. 2002) to the data for each species (birds in the Chesapeake Bay Lowlands, anurans in the Chesapeake Bay Lowlands, and butterflies in the central and western Great Basin), sampling design, and year. For all species we fit models that represented alternate hypotheses about the variation in detection probability (p) among sites and surveys, but did not use covariates to model variation in occupancy (ψ) among sites. We fit a model with constant p (ψ [.] p [.], where “.” indicates no variation in the parameter), and a model with survey-specific p_j (ψ [.] p [t], where j indexes survey and is treated as a categorical variable with three levels).

For birds, we also fit models that included one of four survey-specific covariates: time (number of minutes) since sunrise, Julian date, observer identity, and detection history. Detection history refers to the series of species-specific detections (represented as 1s) and non-detections (represented as 0s). For example, the detection history of a species that was detected on the first and third visits but not detected on the second visit would be 101. The lag between sunrise and initiation of a survey could affect p because song frequency decreases as time since sunrise increases (Skirvin 1981). We included Julian date to capture variation in p throughout the breeding season (Best 1981, Skirvin 1981). We included observer identity because the ability to detect a given species varies among observers (Bart 1985, Diefenbach et al. 2003, Alldredge et al. 2007, Simons et al. 2007, Miller et al. 2011). Inclusion of detection history allowed estimates of p to differ between sites at which the species previously had been detected or not detected (MacKenzie et al. 2006). Higher estimates of p at the former suggest dependence among observations.

For anurans, we also fit models that included one of four survey-specific covariates: Julian date, time since sunset, temperature ($^{\circ}\text{C}$), and log temperature (a pseudo-threshold [Scherer et al. 2012], log [$^{\circ}\text{C}$]). We included a fifth survey-specific covariate, number of days since above-average rainfall, for species that breed during the middle and late breeding season. We included Julian date to account for temporal variation in vocalization. We included time since sunset

because vocalization frequency may vary throughout the night. We included temperature because vocalization frequency may decrease as temperature decreases. We included days since above-average rainfall because species that breeding during the middle and late breeding season vocalized more frequently after a major rain event. We did not include observer identity as a covariate because there was some consistency in observers among years. We did not include detection history as a covariate because, unlike birds, anurans are stationary during the breeding season.

For butterflies, we fit models with constant and survey-specific p . We also fit models that included one of two survey-specific covariates, relative abundance of nectar and relative abundance of mud.

We derived model-averaged estimates of ψ (Burnham and Anderson 1998) and unconditional 95% confidence intervals. We considered differences in p or p^* (the probability that a given species was detected at least once during three surveys) between single-day and multiple-day to be statistically significant if the 95% confidence interval centered on the difference between the single- and multiple-day p or p^* estimate did not include zero (Schenker and Gentleman 2001).

p^* identifies potential reductions in precision of ψ estimates between sampling designs because naive ψ is divided by p^* to estimate ψ (MacKenzie et al. 2006). As p^* decreases, ψ increases. To calculate p^* , we first compared model-averaged and site- and survey-specific p . When the mean and median of site- and survey-specific estimates of p were similar, we used estimates of p from the model with constant p to estimate p^* .

We examined whether the output of each model included evidence of lack of convergence or estimation problems (e.g., extremely large standard errors). If we observed either of the latter in at least one model for a given species in either survey year, we removed the species from further analyses for that year. In other words, we restricted our inferences to those species for which all models converged in both designs in one year.

We report the percentage (mean \pm SE) of species for which occupancy models converged and produced reasonable estimates (i.e., 95% confidence interval did not range from zero to one and other diagnostics did not indicate estimation problems). We fit all models with R Mark (Laake 2013) in the R statistical software package (R version 2.15.2, <http://www.r-project.org/>, accessed 15 Dec 2013).

Simulations. To evaluate potential biases inherent in single-day or multiple-days sampling designs, we simulated data in which detection probability and occupancy were constant but the species' availability varied. We based known, taxonomic group-specific detection probabilities and occupancy on the average estimate across all species for which models converged. The availability process is random in the multiple-days design. However, the availability process is Markovian in the single-day design; if a given species is available during the first survey, it is more likely to be available during the second and third survey. As a result, heterogeneous detection histories (e.g., 010, 100, 101) are more common in data from the multiple-days design and homogeneous detection histories (e.g., 000, 111) are more common in data from the single-day design.

For each design, we varied availability in 0.1 increments from 0.1 to 1.0. To estimate ψ and p^* for each of the ten availability values, we first created detection histories for 130 sites and repeated this process 100 times. Presence or absence was random for each survey in the multiple-days design and the first survey in the single-day design. The second and third surveys in the single-day design had the same state as the first survey. For each of 100 detection histories we then estimated ψ and p^* and derived a final mean and standard deviation for each availability value on the basis of the 100 runs. We ran all models with R Mark (Laake 2013) in the R statistical software package (R version 2.15.2, <http://www.r-project.org/>, accessed 15 Dec 2013).

Estimation of species richness of multiple taxonomic groups on the basis of a single group

Matching of survey data. Several of our analyses required comparisons of point-based surveys of birds with transect-based surveys of butterflies. To generate spatially comparable survey units, we buffered butterfly transects by 100 m (the radius of the bird points) on either side and compiled records of all bird species recorded at points within the buffered butterfly transect. We excluded all bird points that did not fall within a buffered butterfly transect and all butterfly transects that included no bird points. Differences in the years in which birds and butterflies were surveyed led to differences among models with respect to the years of data that were used for indicator selection and evaluation (see below).

Environmental data. We evaluated whether 11 environmental variables—canyon area, elevation, terrain ruggedness, minimum temperature, maximum temperature, precipitation, prevalence of canopy, prevalence of shrubs, number of large trees, riparian fragmentation, and riparian cover—explained or predicted the species richness of birds. We selected these variables on the basis of their relevance to the Great Basin avifauna (Dobkin and Wilcox 1986, Ehrlich et al. 1988). We evaluated seven environmental variables relative to the species richness of butterflies that one reasonably might expect to be relevant to that taxonomic group in the Great Basin (Boggs and Ross 1993, Fleishman et al. 2003): sampled area, mean elevation, terrain ruggedness, maximum temperature, precipitation, abundance of nectar, and abundance of mud. To estimate canyon area (ha), we connected the centroids of the points along the minor road or trail in each canyon (on or near which we sampled) and buffered 100 m on either side of that line. We calculated elevation (m), which we derived from a 10-m digital elevation model (DEM), as the mean elevation within 100 m of the center of the point (birds) or within the transect buffered 25 m on either side (butterflies). We calculated terrain ruggedness (Riley et al., 1999), which we also derived from a 10-m DEM, as the mean within the 100-m point (birds) or within 30-m circular neighborhoods over the transect (butterflies). We derived the three weather variables at 4-km resolution from the Parameter–elevation Relationships on Independent Slopes Model (PRISM) for the water year (October–September) in which a given survey was conducted. We calculated maximum and minimum temperature as the mean of mean maximum (or minimum) monthly temperature ($^{\circ}\text{C}$), and precipitation as the sum of the monthly precipitation totals. We measured prevalence of canopy and shrubs as the proportion of the 21 sampling locations in a given point at which canopy or shrubs was present. Trees were classified as large if their diameter at breast height (dbh) or basal diameter was ≥ 16 cm. We calculated riparian fragmentation at the extent of the canyon (30-m resolution) as the mean distance from each riparian cell to the nearest riparian cell within the sampled area of the canyon. Proportion of

riparian cover within each point was derived from measures of the normalized difference vegetation index (NDVI) (generally >0.25) in National Agriculture Imagery Program (NAIP) aerial images (<https://lta.cr.usgs.gov/NAIP>).

We used year-specific values for variables that were highly dynamic and for which we had multiple years of data (temperature, precipitation, and abundance of nectar and mud). The topographic variables we measured were static over the time period of our work. Values of our vegetation variables unlikely to change substantially over less than a decade in the absence of major disturbances.

Indicator selection. We used Bayesian model selection to identify sets of five indicator species that explained the greatest proportion of variation in species richness (*indicator selection*). Our primary focus was the development of a transferable method for identifying indicator species; we did not necessarily expect that the same set of species would be associated with species richness in all ecological or management circumstances. We fitted a log-linear Poisson regression model, but estimated model coefficients with a reversible-jump Markov chain Monte Carlo sampler, which allows variables to be removed from or added to the model during model fitting (Lunn et al. 2008). This method estimates the posterior probability of inclusion of each candidate indicator species. We identified the five species with the highest posterior probabilities of inclusion.

The response variable, species richness of birds or species richness of butterflies, included all species detected in the specified subregion or time period. We restricted candidate indicator species to those detected in both subregions or both time periods because only these can serve as transferable indicators.

Model fitting. We fitted random forest models with either the five indicator species, all of the environmental variables, or the five indicator species and all of the environmental variables (*full models*) (Figure 8). We fitted models with indicator species only and with both indicator species and environmental variables to account for possible confounding between indicator species and environmental variables. We fitted each model variant ten times (hereafter referenced as *ten iterations*). We report results as averages across the ten iterations.

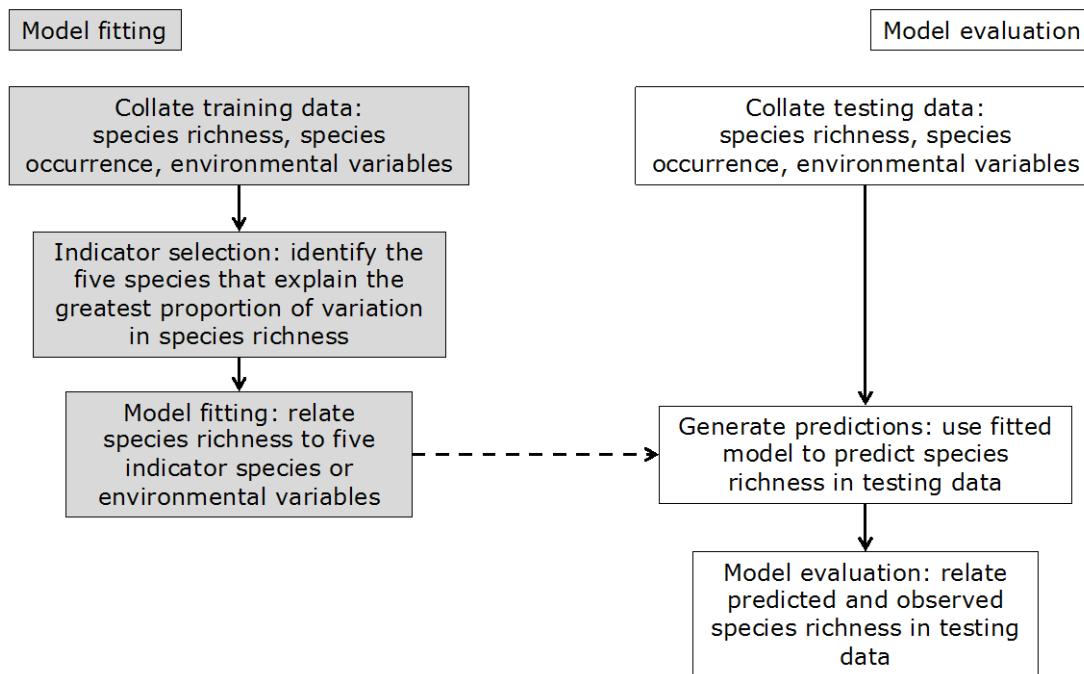


Figure 8. Main steps in the model fitting and model evaluation process.

The fitted models included a different value of the response variable for each year. For example, if we built a model with data collected from 2012–2014, the model included three values of species richness for each location. We fitted models with and without spatial and temporal random effects to assess whether correlations among locations or years affected model fit. The inclusion of random effects substantially reduced the accuracy of external tests of the fitted models. Therefore, we report results for models fitted without these terms.

Model evaluation. We used the three types of fitted models to estimate species richness in new locations or at future times (*model evaluation*, i.e., external evaluation or prediction [Elith and Leathwick 2009]; in the case of the indicator species-only models, we reference *indicator evaluation*) (Figure 8).

We conducted separate evaluations of the spatial and temporal transferability of our fitted models because we wished to avoid confounding the two types of transferability. For evaluations of spatial transferability, we conducted indicator selection in one zoogeographic subregion (i.e., the central or western Great Basin), and indicator evaluation in the other subregion. For evaluations of temporal transferability, we conducted indicator selection with data from a subset of the sampled years in one subregion, and indicator evaluation with data from a later subset of the sampled years in the same subregion. For each model variant, we used each of the ten fitted

random forest models to predict species richness in the other subregion or for the later time period. We assessed model accuracy with r^2 values (based on Pearson's r) between predicted and observed species richness.

We present and discuss the number and identity of indicator species and environmental variables included in the models in which ≥ 0.25 of the variation in the response variable was predicted. We used this threshold, which is arbitrary but has been recommended (Møller and Jennions 2002), to simplify reporting of the results. Results at other thresholds (e.g., 0, 0.50) were not substantially different.

Theory and practical application of occupancy models: hierarchical models of occupancy

We used a dynamic occupancy model to evaluate associations of covariates with occupancy, persistence, colonization, and detection of birds in the Chesapeake Bay Lowlands and central and western Great Basin while accounting for the possibility of false absences. We considered the true presence or absence of each of J species, each of which was a member of one of G guilds, at each of K points, in each of T time steps to be a partly observed state variable $z_{j,k,t}$, which is equal to one if species j is present at point k in time step t , and equal to zero otherwise. Because we used a model specification that marginalized over the latter state variable, we directly modeled $\psi_{j,k,t}$, the probability of occurrence.

Observation model

We represented the detection data from the Chesapeake Bay Lowlands as $y_{j,k,t}$, which indicates whether species j was detected at point k during year t . Three surveys were conducted at each point in each year, so $y_{j,k,t}$ was a vector of length 3 in which each element had a value of 0 (not detected) or 1 (detected). Following the likelihood formulation of Royle and Dorazio (2008), and marginalizing the latent occupancy state variable, our likelihood function was

$$[y_{j,k,t} \mid \psi_{j,k,t,i}, p_{k,i}] = \psi_{j,k,t} \prod_{i=1}^3 \text{Bernoulli}(y_{j,k,t,i} \mid p_{j,k,i}) + I_{(\sum_{i=1}^3 y_{j,k,t,i}=0)}(1 - \psi_{j,k,t})$$

where $\psi_{j,k,t}$ is the probability of species j occurring at point k in year t , $p_{j,k,i}$ is the probability of detection on survey i , $I_{(\sum_{i=1}^3 y_{j,k,t,i}=0)}$ is an indicator function that takes on the value 1 only if $\sum_{i=1}^3 y_{j,k,t,i} = 0$ and is zero otherwise, and square brackets represent the probability function (i.e., a probability mass function $\text{Pr}(Y = y|\theta)$ for discrete variables or a probability density function $p(y|\theta)$ for continuous variables, where θ represents parameters of the distribution of the random variable Y .

We represented the detection data from the central and western Great Basin as $y_{i,j}$, which is the number of times species j was detected during year i , bounded between 0 and n_j , the number of

surveys in year i . Following the likelihood formulation of Royle and Dorazio (2008), and marginalizing the latent occupancy state variable, our likelihood function for surveys $i = 1, \dots, n$ and species $j = 1, \dots, J$ was

$$[y_{i,j} | \psi_{j,k_i,t_i}, p_{k_i}] = \psi_{j,k_i,t_i} \text{Binomial}(y_{i,j} | p_{k_i}; n_i) + I(y_{i,j}=0)(1-\psi_{j,k_i,t_i}),$$

where ψ_{j,k_i,t_i} is the probability of species j occurring at point k_i in year t_i , p_j is the probability of detection, $I(y_{i,j}=0)$ is an indicator function that takes on the value 1 only if $y_{i,j} = 0$ and is zero otherwise, and square brackets represent the probability function (i.e., a probability mass function $\text{Pr}(Y = y|\theta)$ for discrete variables or a probability density function $p(y|\theta)$ for continuous variables, where θ represents parameters of the distribution of the random variable Y .

Process model. The process model has three components: initial occupancy, colonization, and extinction. Colonization and extinction determine occupancy beyond the initial time step. For all of these components, we created a set of covariates that reasonably could be expected to be associated with occupancy of each guild (allowing relations to vary among guilds).

For initial occupancy in the Chesapeake Bay Lowlands, we included the following point-level covariates: number of snag saplings; cover of leaf litter; volume of downed woody debris; number of deciduous trees in the subcanopy; number of deciduous trees in the canopy; number of deciduous saplings; number of coniferous saplings; mean canopy height within 100 m of the point center; structural heterogeneity between 0 and 3 m height within 100 m of the point center; proportion of riparian cover within 500 m of the point center; proportion of mesic deciduous or mixed tree cover within 500 m of the point center; length of forest edge within 500 m of the point center; proportion of low density, moderate density, and high density development within 500 m of the point center; and proportion of conifer cover within 500 m of the point center. We embedded this information in a site-level design matrix X_S in which the columns contained centered and scaled continuous covariates that interacted with guild. This design matrix therefore represented the interactions of three guilds with 16 covariates, yielding 48 columns and $K \times G$ rows, where each row represented a site by guild combination. Because occupancy varies among species, we included a species-specific adjustment for initial occupancy, α_j . Therefore, our submodel for initial occupancy was

$$\text{logit}(\psi_{j,k,1}) = \mu_{\psi_1} + \alpha_j^{(\psi)} + X_S^{(g_j,k)} \beta_{\psi_1}$$

where μ_{ψ_1} is a global intercept, $\alpha_j^{(\psi)}$ is a species specific adjustment, β_{ψ_1} is a parameter vector of length $K \times G$, and $X_S^{(g_j,k)}$ is a row vector from X_S corresponding to point k and the guild of species $j(g_j)$.

For subsequent time steps $t > 1$, we modeled detection probability with an autoregressive formulation that included a persistence probability from time step $t - 1$ to t ($\phi_{j,k,t-1}$) and a colonization probability (the probability that a point unoccupied in $t - 1$ is occupied in time t): $\gamma_{j,k,t-1}$:

$$\psi_{j,k,t} = \psi_{j,k,t-1} \phi_{j,k,t-1} + (1 - \psi_{j,k,t-1}) \gamma_{j,k,t-1}$$

To explore potential environmental associations with colonization and extinction, we also modeled ϕ and γ as functions of the same point-level covariates introduced for the initial occupancy submodel. We also included species-specific adjustments through random effects to account for variation in colonization and extinction probabilities among species. The submodels for persistence and colonization therefore were

$$\text{logit}(\phi_{j,k,t}) = \mu_\phi + X_{S(jk)} \beta_{\phi S} + \alpha^{(\phi)}$$

$$\text{logit}(\gamma_{j,k,t}) = \mu_\gamma + X_{S(jk)} \beta_{\gamma S} + \alpha^{(\gamma)}$$

where $\alpha^{(\phi)}$ and $\alpha^{(\gamma)}$ are species-specific adjustments for persistence and colonization, β terms represent parameter vectors, and μ terms represent global intercepts.

We allowed for point-level variation in detection probabilities by modeling the effect of log-transformed wind speed, time since sunrise, and days since May 1, centered and scaled to comprise three columns in a detection design matrix X_p , which had $K \times T \times 3$ rows, one for each point by year by survey combination. We also included a species-specific adjustment in detection probability:

$$\text{logit}(p_{j,k,t}) = \mu_p + X_{p(jk)} \beta_p + \alpha^{(p)}$$

For initial occupancy in the central and western Great Basin, we included the following covariates: mountain range (Shoshone, Toiyabe, Toquima, and Monitor in the central Great Basin; Wassuk, Sweetwater, and Sierra in the western Great Basin), canopy prevalence (the number of presences divided by the number of samples, generally 21 per point), elevation (mean elevation within the center of the point, derived from a 10-m digital elevation model), mean canopy cover, mean coniferous canopy cover, mean riparian canopy cover, rabbitbrush incidence (number of presences divided by number of samples), riparian fragmentation (calculated as the mean distance from each riparian cell to the nearest riparian cell within the sampled area), sagebrush prevalence (number of presences divided by number of samples), and terrain ruggedness. We embedded the covariate information in a point-level design matrix X_S in which the columns contained indicator variables for categorical covariates (such as mountain range), and centered and scaled continuous covariates, both interacting with guild.

The full design matrix represented the interactions of three guilds with each of the 12 covariates (36 columns) and $K \times G$ rows, where each row represents a point-by-guild interaction. Because occupancy varies among species, we included a species-specific adjustment for initial occupancy, α_j . Our submodel for initial occupancy was

$$\text{logit}(\psi_{j,k,1}) = \mu_{\psi 1} + \alpha_j + X_{S(gj,k)} \beta_{\psi 1},$$

where $\mu_{\psi 1}$ is a global intercept, α_j is a species specific adjustment, $\beta_{\psi 1}$ is a parameter vector of length $K \times G$, and $X_S(gj,k)$ is a row vector from X_S corresponding to point k and the guild of species $j(gj)$.

For subsequent time steps $t > 1$, we modeled detection probability with an autoregressive formulation that included a persistence probability from time step $t - 1$ to t : $\phi_{j,k,t-1}$, and a

colonization probability (the probability that a point unoccupied in $t - 1$ is occupied in time t):
 $\gamma_{j,k,t-1}$:

$$\psi_{j,k,t} = \psi_{j,k,t-1}\varphi_{j,k,t-1} + (1 - \psi_{j,k,t-1})\gamma_{j,k,t-1}.$$

To explore spatial and temporal associations with colonization and extinction, we also modeled φ and γ as functions of covariates.

For the central and western Great Basin, we included both the same point-level covariates introduced for the initial occupancy submodel and a new set of spatially and temporally dynamic covariates at the year level: maximum air temperature, minimum air temperature, and total precipitation, all from March through May. These three covariates crossed with the three guilds generated 9 variables that comprised the columns of a dynamics design matrix X_d , which had $K \times G \times (T - 1)$ rows (among T time steps, $T - 1$ colonization and persistence events are possible). The submodels for persistence and colonization thus were

$$\begin{aligned} \text{logit}(\varphi_{j,k,t}) &= \mu_\varphi + X_s^{(jk)}\beta_{\varphi_s} + X_d^{(gj,k,t)}\beta_{\varphi_d} \\ \text{logit}(\gamma_{j,k,t}) &= \mu_\gamma + X_s^{(jk)}\beta_{\gamma_s} + X_d^{(gj,k,t)}\beta_{\gamma_d} \end{aligned}$$

where $X_d^{(jkt)}$ extracts the row from X_d corresponding to the guild of species j (g_j), point k , and time step t , β terms represent parameter vectors, and μ terms represent global intercepts.

We allowed for point-level variation in detection probabilities by modeling the effect of canopy cover, shrub cover, and terrain ruggedness, centered and scaled to comprise three columns in a detection design matrix X_p , which had K rows, one for each point:

$$\text{logit}(p_k) = \mu_p + X_p^{(k)}\beta_p$$

Parameter model. To complete our model specifications for the Chesapeake Bay Lowlands and central and western Great Basin, we specified prior distributions for all remaining parameters as follows. All of the global intercepts ($\mu_\psi, \mu_\varphi, \mu_\gamma$) received $\text{Normal}(\mu = 0, \sigma = 1.5)$ priors, which led to nearly uniform prior distributions on the probability scale. The species-specific adjustments for initial occupancy were treated as normally distributed random effects with unknown variance: $\alpha \sim \text{Normal}(0, \sigma_\alpha)$, with $\sigma_\alpha \sim \text{Normal}(0, 1)$. For our three detection coefficients, we assigned conservative priors: $\beta_p \sim \text{Normal}(0, 1)$.

Across the initial occupancy, persistence, and colonization submodels, we had well over 100 β coefficients to estimate. However, we expected a priori that the majority of these coefficients would be nearly zero. Therefore, we used a scale mixture prior, adapted from the horseshoe prior, which induces sparseness by shrinking estimates toward zero while allowing for some of the coefficients to be far from zero. Concatenating $\beta_\psi, \beta_{\varphi_s}, \beta_{\varphi_d}, \beta_{\gamma_s}$, and β_{γ_d} into one vector β^* , we assumed the following scale mixture prior for parameters $l = 1, \dots, L$, where L is the total number of coefficients in β^* :

$$\begin{aligned}
\beta_1^* &\sim \text{Normal}(0, \tau \lambda_1) \\
\lambda_1 &\sim \text{Student-t}(0, 1, \eta = 3) \\
\tau &\sim \text{Normal}(0, 1)
\end{aligned}$$

This prior distribution is similar to the original horseshoe prior, but uses a lighter tailed Student-t distribution for λ rather than a Cauchy distribution, which is more reasonable under the logit link function.

Use of occupancy as a surrogate measure of species richness: estimation of the occupancy of butterflies in diverse biogeographic regions

We used single-season occupancy models to analyze the data collected from all transects and on all visits during 2013 and 2014 for 13 species of butterflies in the Chesapeake Bay Lowlands and 15 species each in the central and western Great Basin. We generally restricted our analyses to species that were detected in $\geq 30\%$ and $\leq 70\%$ of the transects in each year and that are not migrants, highly vagile (e.g., thousands of meters), or do not complete their entire life cycle in the ecosystem. We also modeled single-season occupancy of the 15 species in the central Great Basin in 1995.

We fit two parameterizations (MacKenzie et al. 2002, Kendall et al. 2013) of the single-season occupancy model. Both include the parameters ψ_i , the probability that a given species occupies transect i , and p_{ij} , the probability that the species is detected given that it is present on transect i during visit j . The Kendall et al. (2013) model also allows a single entry and exit of the species from each transect during the sampling period; the probabilities of entry and exit between visits j and $j + 1$ are denoted as β_{ij} and d_{ij} , respectively. p_{ij} may vary during the period in which the species is available.

We fit models to the occupancy data in two stages. In the first stage, we evaluated submodels of p_{ij} , β_{ij} , and d_{ij} , and tested the assumption of closure. For both parameterizations, the sets of submodels of p_{ij} included effects of categorical abundance of nectar, mud (in the Great Basin), or both. In all cases, we used the highest-abundance class of nectar or mud as the intercept.

We also included a fixed effect of visit (i.e., we estimated p_{ij} for each survey) in the submodels. Furthermore, the submodels included additive effects of nectar and visit and of mud and visit. For the models in which the closure assumption was relaxed, we estimated β_{ij} and d_{ij} as linear and quadratic functions of visit. We specified full models that included every combination of the submodels of p_{ij} , β_{ij} , and d_{ij} with an intercept-only submodel of occupancy. We used Akaike's Information Criterion adjusted for small sample sizes (AIC_c) and Akaike weights (w_m), where m indexes models, to compare submodels of p_{ij} , β_{ij} , and d_{ij} (Burnham and Anderson 2002). We retained all models from the first stage of modeling with AIC_c values within 2 units of the highest-ranked model and included them in the second stage of modeling.

In the second stage of modeling, we evaluated submodels of ψ_i . The set of submodels included effects of each covariate and several ecosystem-specific interactions. We combined all

submodels of ψ_i with the submodels of other parameters from the model that was ranked highest in the first stage. Because many models that included covariates generated highly imprecise occupancy estimates, we report ψ_i from the intercept-only submodel.

We standardized and centered all continuous covariates. We calculated Pearson product-moment correlations between continuous covariates. We did not include two continuous covariates in a given model if their correlation coefficient was ≥ 0.60 . We examined box-and-whisker plots, created in R (R Core Team, 2013), to assess correlations between continuous and categorical covariates. We used the plots to anticipate potential confounding effects of multicollinearity. When a strongly supported model included both a continuous and a categorical covariate, we examined whether the magnitude or direction of regression coefficients in the latter model and in models that included each of those covariates alone was considerably different. We included a maximum of two covariates in additive models.

We characterized the strength of association between response variables and covariates on the basis of the AIC_c values of the models in which they were included and the degree to which estimates of the 95% confidence intervals (CIs) of the regression coefficients overlapped zero. If a covariate was included in the model with the lowest AIC_c , or in a model with an AIC_c value within 2 units of the model with the lowest AIC_c , we considered it to be associated with p_{ij} or ψ_i and report it here. We considered the strength of association of a covariate with p_{ij} or ψ_i to be greater if its CIs did not overlap zero than if its CIs overlapped zero. We report associations with continuous covariates as regression coefficients and associations with categorical covariates as effect sizes.

When data are limited or probabilities approach 0 or 1, parameters may not be estimated correctly. Evidence of incorrect estimates includes noticeably high values of parameters or their standard errors and estimates of standard errors that are near zero. We examined estimates of model parameters and used the diagnostics in Program MARK to identify potentially questionable estimates. We also considered regression coefficients or effect sizes with absolute values ≥ 10 to be questionable.

Use of occupancy as a surrogate measure of species richness: environmental associations with multiple states of anuran occupancy

For each species, we combined the data from the wetland surveys in 2011 and 2012 and fit both a single-season, single-state occupancy model (MacKenzie et al. 2002) and a single-season, multiple-state occupancy model (Nichols et al. 2007). We fit models to the data for three species: Fowler's toad (*Anaxyrus fowleri*), Cope's gray tree frog (*Hyla versicolor*), and spring peeper (*Pseudacris crucifer*). Before fitting the single-state model, we modified the occupancy data for each species by replacing all calling indices with ones, indicating simply that the species was detected. For the multiple-state analyses, we treated the calling-index values as estimates of the relative abundance. Therefore, each wetland could be unoccupied, occupied by a population capable of producing a low calling-index value, or occupied by a population capable of producing a high calling-index value. We pooled two values of the calling index (either 1 and 2 or 2 and 3), which resulted in two possible occupancy states. We evaluated covariates of

wetlands and the surrounding areas at three spatial extents that corresponded to breeding, migration, and dispersal.

We evaluated four covariates that might be associated with occupancy and relative abundance during the breeding phase of the life cycle: wetland area (m^2), wetland perimeter, percentage of canopy cover within a 10-m buffer around the wetland perimeter, and whether the wetland was covered by $< 50\%$ or $\geq 50\%$ emergent vegetation emergent vegetation.

We considered a 1-km buffer around the wetland perimeter as the extent of migration. Within that buffer, we estimated percentage of upland forest cover, degree of forest aggregation, and stream density (a proxy for riparian and mesic-forest cover) in 100-m increments. We measured forest aggregation with the clumpiness index (FORCLUMP) in Fragstats 4.0, which estimates the degree of fragmentation of a land-cover type independent of the area of that land-cover type.

We considered a 1.5–5 km buffer around the wetland perimeter as the extent of dispersal. Within that buffer, we estimated percentage of wetland area, density of highways with high traffic volume (km/km^2), effective mesh size (ha), and percentage of impervious surface in 0.5-km increments. Effective mesh size is an estimate of the probability that two random points in a given area can be connected without encountering a barrier (in this case, a road), and is interpreted as the expected size of a patch in an area with fragmented land cover.

We first fit single-covariate models in which we included values of the covariate at all spatial extents or increments. We considered an association between the covariate and the response variable to be supported by the data if it was included in a model with an AIC_c value that was smaller than the intercept-only model and if the 95% confidence interval around the estimates of the regression coefficient for the covariate did not include 0. We retained these covariates and fit multiple-covariate models. We used values of the covariate at the distance and with the functional form that had the lowest AIC_c. We fit the multiple-covariate models with every possible combination of two or more covariates. However, we computed Pearson's correlation coefficients for all pairs of covariates and did not include covariates in the same model if the absolute value of the correlation coefficient was > 0.60 .

Responses of songbird occupancy to environmental change

We assessed the level of forest fragmentation in coastal and inland Virginia on the basis of 30-m data from the Landscape Fire and Resource Management Planning Tools Project (LANDFIRE) (2012). We used the amount of forest edge as a measure of fragmentation. We assumed that areas classified by LANDFIRE as forest, grassland, row crop, and rural were relevant to deer, and measured the mean length per 1 km^2 plot of edges between forest and grassland, row crops, or rural areas. We also calculated road density (km per km^2) in each region; road density often is correlated with deer density (Lovely et al. 2013). As an independent index of deer abundance for the two regions, we divided the number of harvested deer (2004–2013, data provided by the Virginia Department of Game and Inland Fisheries) by forest area in each county that intersected our sites.

We used two tests to assess differences in deer use between coastal and inland Virginia. We used a Wilcoxon rank sum test to compare the number of deer pellets in coastal and inland Virginia, and a paired *t*-test to compare the number of deer harvested. We determined whether edge density differed on the basis of whether 95% confidence intervals overlapped. We estimated both bird and deer pellet densities (individuals and pellets ha⁻¹, respectively) with Multicovariate Distance Sampling (MCDS) in Distance 6.0 software (Thomas et al. 2010). We determined whether detection probabilities differed between species and guilds on the basis of whether 95% confidence intervals overlapped. We grouped birds into three guilds: species that nest in understory shrubs and glean understory foliage, species that nest in the canopy and feed on open ground, and species that nest in the canopy or cavities and either feed in the canopy or sally aerially (Ehrlich et al. 1988). We restricted species-level analyses to passerines that nest in forest and for which we had ≥ 60 detections (Thomas et al. 2010). The latter restricted our species-level analysis to coastal Virginia. We used Spearman's rank correlation to test whether deer and bird densities were correlated.

Partitioning drivers of beta diversity

Calculation of turnover and nestedness. We calculated beta diversity from detection data at two spatial resolutions: points or transects and canyons. We calculated temporal and spatial beta diversity separately. We defined temporal beta diversity as the variation in species' identities among years at one point, transect, or canyon. We defined spatial beta diversity as the variation in species' identities among all points or transects within a canyon, or among all canyons within a mountain range, in a given year.

We partitioned beta diversity into two components—turnover and nestedness—with the additive partitioning method outlined in Baselga (2010). We based estimates of turnover and nestedness on Sørensen dissimilarity, which reflects the proportion of species shared between two assemblages. Additive partitioning uses the Simpson dissimilarity index, an estimate of beta diversity that is insensitive to variation in species richness. Thus, the Simpson dissimilarity index reflects turnover. Total beta diversity, defined as the Sørensen dissimilarity, comprises variation due to turnover and variation due to nestedness. Therefore, the difference between the Sørensen and Simpson dissimilarity indices is the contribution of nestedness to total beta diversity (Baselga 2010). Total beta diversity ranges from zero to one, and turnover and nestedness together sum to total beta diversity. Therefore, turnover and nestedness also range from zero to one.

Because beta diversity estimates calculated on the basis of different numbers of surveys are not directly comparable, we used subsampling to compare beta diversity estimates from different locations or taxonomic groups. For each temporal or spatial unit for which we wished to calculate beta diversity (typically three to ten surveys), we randomly sampled 100 pairs of surveys and used the average pairwise beta diversity over all pairs as our estimate of beta diversity for that set of surveys. The result of this process was estimates of temporal turnover and nestedness at each point or transect and canyon, and estimates of spatial turnover and nestedness among all points within each canyon and among all canyons within each mountain range.

Null models of turnover and nestedness. We used a null model to estimate beta diversity in the absence of any ecological structuring (e.g., environmental filtering or limiting similarity). For each set of surveys for which we wished to calculate beta diversity, we randomly sampled 999 pairs of surveys and, for each pair, shuffled the identities of observed species while holding species richness constant. We calculated beta diversity for each shuffled pair and used these 999 values to estimate an expected distribution of beta diversity values in the absence of ecological structuring of species' identities.

We defined all observed beta diversity estimates less than 2.5% or greater than 97.5% of the null-model estimates as evidence of ecological structuring in beta diversity. Turnover values less than 2.5% of the null-model estimates indicate more-consistent species composition than would be expected in the absence of ecological processes, whereas values greater than 97.5% of the null-model estimates indicate more-variable species composition than would be expected in the absence of ecological processes. Nestedness estimates less than 2.5% of the null-model estimates indicate less overlap in composition among assemblages than would be expected in the absence of ecological processes, whereas estimates greater than 97.5% of the null-model estimates indicate more overlap in composition among assemblages than would be expected in the absence of ecological processes.

Statistical comparison of spatial resolutions and zoogeographic regions. We used a Bayesian linear model to estimate differences in turnover and nestedness between the point or transect resolution and the canyon resolution, and to compare turnover and nestedness between the central and western Great Basin. The model was

$$y_i = \alpha + \beta_{west} I(west) + \beta_{canyon} I(canyon) + \square, \quad (1)$$

where y_i is the observed turnover or nestedness for survey i , α is the mean turnover or nestedness in the central Great Basin at the point or transect resolution, β_{west} is the deviation from α in the western Great Basin, $I(west)$ is an indicator variable equal to one if observation i is in the western Great Basin and zero otherwise, β_{canyon} is the deviation from α at the canyon resolution, $I(canyon)$ is an indicator variable equal to one if observation i is estimated at the canyon resolution, and \square is the residual variation in turnover or nestedness for observation i .

We assigned uniform priors on $[0, 1]$ to α , uniform priors on $[0 - \alpha, 1 - \alpha]$ to β_{west} , and uniform priors on $[0 - \alpha - \beta_{west}, 1 - \alpha - \beta_{west}]$ to β_{canyon} . We assigned a Gaussian prior to \square , with zero mean and standard deviation uniformly distributed on $[0, 1]$. These priors reflected that turnover and nestedness estimates were between zero and one in all cases. We fitted the model defined in eq. (1) in WinBUGS 1.4 with the R2WinBUGS package in R. We summarized all outputs in R.

Statistical analysis of the relation between beta diversity and environmental variables. We used a random forest model to determine whether and how turnover and nestedness of birds and butterflies in the central and western Great Basin changed along environmental gradients. Random forests use recursive binary splits to generate a large number of tree-like structures (a forest), each of which partitions variation in a response variable (e.g., turnover or nestedness) into groups on the basis of a set of covariates (e.g., environmental variables). Random forests incorporate high-level interactions and nonlinear effects, so are well suited to identifying complex ecological relations when there are a moderate to large number of covariates. The fitted

random forest model is based on the consensus output over many trees; we used 500 trees in all analyses.

We assessed model fit as the r^2 value, based on Pearson's r , between observed and fitted beta diversity estimates. We used ten-fold cross validation to determine the robustness of fitted relations. In cross-validation, one partitions the data into multiple similar-sized subsets of all observations (folds), and fits the model with each fold removed in turn (holdout data). Fitted models are used to project the response variable for the holdout data, and cross-validated r^2 values are based on the correlation between predicted and observed values. Cross-validation identifies overfitted models because such models generate poor predictions for holdout data.

We plotted fitted models on the basis of partial dependence plots, which estimate the marginal effect of a given covariate on the response. Marginal effects are estimated by holding the value of the covariate constant while fitting random forest models with a range of values for other covariates. The marginal effect is estimated as the average association between the covariate and the response variable averaged over all model runs. Partial dependence plots do not display the multilevel interactions supported by random forest models, but approximate the shape of fitted relations. We fitted random forest models with the randomForest package in R.

Results and Discussion

Hierarchical estimates of species richness

The results of this analysis provide information on spatial scales at which it may be most relevant to assess and monitor native birds and butterflies and project responses of these taxonomic groups to land use and management, especially if the response variable is species richness or occupancy, throughout the Intermountain West. Birds and butterflies are two of the most commonly monitored faunal groups, and well over half of the Intermountain West is managed by federal agencies, including the Department of Defense. The results also support the design of effective, cost-efficient, and spatially transferable methods for assessment and monitoring of native species; and evaluation of theories regarding relations between species richness and environmental variables.

The central Great Basin bird data encompassed 15 years of surveys, with 4-21 points per canyon and 27 canyons. The number of years a given point was surveyed ranged from 6 to 15. The western Great Basin bird data encompassed three years of surveys, with 8-20 points per canyon and 13 canyons. We treated canyon as an indicator variable and identified 23 covariates, nine at the canyon level and 13 at the point level, that reasonably could be expected to be associated with species richness of birds. We also included number of survey years as a covariate.

At the point level in the central Great Basin, the relation between number of survey years and cumulative species richness was 0.15. The adjusted r-squared values of models of point-level species richness as a function of point-level covariates, canyon level-covariates, or both were 0.24, 0.20, and 0.38, respectively. Significant point-level covariates were elevation (linear), number of years sampled, canopy cover, shrub cover, and mean minimum temperature. Significant canyon-level covariates were elevational range, terrain ruggedness within a 500-m buffer, canyon area, and riparian fragmentation. In the model that included covariates at both spatial resolutions, significant covariates were elevation (linear), terrain ruggedness, mean minimum temperature, canopy cover, years sampled, elevational range of the canyon, area of the canyon, and riparian fragmentation. About 21% of the total variation in cumulative species richness occurred among canyons, and about 80% within canyons. The pseudo-r² of the hierarchical model was 0.41. The adjusted r-squared of a model of canyon-level species richness as a function of canyon-level covariates was 0.86. Significant covariates in the latter model were riparian fragmentation, canyon area, terrain ruggedness within a 500-m buffer, and sampled area. These results suggest that birds may perceive and respond to their environment at the level of canyons rather than at the level of the relatively small points typically used to sample extensive areas.

In the western Great Basin, the adjusted r-squared values of models of point-level species richness as a function of point-level covariates, canyon level-covariates, or both were 0.24, 0.14, and 0.26, respectively. Significant point-level covariates were elevation (linear and quadratic), terrain ruggedness, standard deviation of precipitation and of minimum temperature, and canopy cover. Significant canyon-level covariates were elevational range, terrain ruggedness within a 500-m buffer, area of canyon bottom within a 500-meter buffer, and number of snags. In the model that included covariates at both spatial resolutions, significant covariates were elevation

(linear and quadratic), standard deviation of maximum temperature, shrub cover, elevational range of the canyon, canyon-level terrain ruggedness within a 500-m buffer, area of canyon bottom within a 500-meter buffer, and number of snags in the canyon. About 17% of the total variation in cumulative species richness occurred among canyons, and about 83% within canyons. The pseudo- r^2 of the hierarchical model was 0.14. The adjusted r^2 of a model of canyon-level species richness as a function of canyon-level covariates was 0.54. Significant covariates in the latter model were elevational range, riparian cover, and riparian fragmentation. Again, canyons appeared to be a more biologically meaningful unit for breeding birds than points within canyons.

To make an analysis of the central Great Basin butterfly data viable, we reduced the data to two years during which the same set of transects were surveyed. These reduced data included 3-12 transects per canyon and 15 canyons. The western Great Basin butterfly data encompassed 4 years of surveys, with 8-20 transects per canyon and 8 canyons. We treated canyon as an indicator variable and identified 17 covariates, six at the canyon level and 11 at the transect level, that reasonably could be expected to be associated with species richness of butterflies.

In the central Great Basin, the adjusted r^2 values of models of transect-level species richness as a function of transect-level covariates, canyon level-covariates, or both were 0.59, 0.40, and 0.73, respectively. Significant transect-level covariates were transect area, the standard deviation of mean maximum temperature, nectar abundance, and mud abundance. Significant canyon-level covariates were elevational range, terrain ruggedness within a 100-m buffer, and riparian fragmentation. In the model that included covariates at both spatial resolutions, significant covariates were transect area, the standard deviation of mean maximum temperature, nectar abundance, mud abundance, the area of the canyon bottom within a 500-m buffer, and terrain ruggedness within a 100-m buffer. About 48% of the total variation in cumulative species richness occurred among canyons, and about 52% within canyons. Species richness was strongly associated with transect area, nectar abundance, mud abundance, and terrain ruggedness within a 100-m buffer. The pseudo- r^2 of this hierarchical model was 0.60. We included three canyon-level covariates in a multiple-regression model of canyon-level species richness; the adjusted r^2 of this model was 0.57, and species richness was most closely associated with presence or absence of riparian areas.

In the western Great Basin, the adjusted r^2 values of models of transect-level species richness as a function of transect-level covariates, canyon level-covariates, or both were 0.70, 0.23, and 0.71, respectively. Significant transect-level covariates were elevation (both linear and quadratic), mean precipitation, mean minimum temperature, nectar abundance, and mud abundance. One canyon-level covariate, elevational range, was statistically significant. In the model that included covariates at both spatial resolutions, significant covariates were elevation (both linear and quadratic), mean precipitation, nectar abundance, mud abundance, and elevational range of the canyon. About 22% of the total variation in cumulative species richness occurred among canyons, and about 82% within canyons. The pseudo- r^2 of this hierarchical model was 0.64. The number of canyons was too small for us to model canyon-level species richness. However, our results were consistent with the hypothesis that butterflies perceive their environment at smaller spatial extents than birds.

Periodicity of sampling: duration of point counts of birds

The results of this analysis provided knowledge that can facilitate effective, cost-efficient, and geographically transferable methods for sampling native birds. Results of analyses applied to data from the Chesapeake Bay Lowlands, central Great Basin, and western Great Basin were similar despite differences in ecology and land use between the ecosystems. The results also inform assessment of trade-offs between increasing the duration of sampling and increasing the number of locations sampled.

Detection estimates. For $82 \pm 4\%$ (mean \pm SE) of the species in a given ecosystem (Chesapeake Bay Lowlands, central Great Basin, or western Great Basin), models of detection probability that were based on both the 5-min and 8-min counts converged (Table 1). Detection probabilities based on both the 5-min and 8-min counts were ≥ 0.3 for $40 \pm 4\%$ of the species in a given ecosystem (range 24–54%) and < 0.3 for $35 \pm 1\%$ of the species (range 30–40%). The percentage of species with detection probabilities ≥ 0.3 was higher in Chesapeake Bay Lowlands (54% in 2012, 47% in 2013) than in the central Great Basin (24% in 2012, 36% in 2013) or western Great Basin (35% in 2012, 41% in 2013). Increasing the count duration from 5 min to 8 min increased the detection probability to ≥ 0.3 for $6 \pm 1\%$ of the species in a given ecosystem (range 3–7%), but decreased the detection probability to < 0.3 for $2.0 \pm 1\%$ (range = 0–4%) of the species.

Occupancy estimates. We estimated occupancy for 35 species in the Chesapeake Bay Lowlands, 27 species in the central Great Basin, and 37 species in the western Great Basin. Occupancy estimates based on 5-min and 8-min counts were not statistically different for any of these species with detection probabilities ≥ 0.3 . This suggests that a modest extension of the recommended 5-min duration of standardized counts (Ralph et al. 1993, 1995, Matsuoka et al. 2014) is unlikely to affect inferences based on occupancy models.

However, we found that the precision (CV) of occupancy estimates for 97% of the species we examined increased by $12 \pm 2\%$ (range 0–38%) when duration increased from 5 min to 8 min. This suggests a trade-off between count duration and precision and that a modest 3-min increase in count duration can provide more-precise occupancy estimates.

We could not estimate occupancy for 46–76% of the species detected in each ecosystem and year, and our work highlighted the difficulty of modeling occupancy of species with large home ranges or uncommon species. Species with low naïve occupancy (percentage of points occupied, not accounting for imperfect detection) for which models did not converge included those with home ranges larger than the area of the points (~3 ha) (e.g., woodpeckers or corvids), those that rarely occur in the land-cover types we sampled (e.g., synanthropic and wetland species), and those that were rare in our study areas. As a general guideline, MacKenzie and Royle (2005) recommended increasing the number of counts rather than the number of points to maximize the precision of estimates for common species, and increasing the number of points rather than the number of counts to maximize precision for rare species.

Table 1. Total number of species detected in 2012 and 2013 in the Chesapeake Lowlands, central Great Basin, and western Great Basin; the number (percentage) of species for which models did or did not converge; and the number (percentage) of species for which detection probabilities (p) based on 5-min and 8-min counts were either ≥ 0.3 or < 0.3 . Percentages are based on the total number of species detected within a given year and ecosystem.

	Chesapeake Bay Lowlands		central Great Basin		western Great Basin	
	2012	2013	2012	2013	2012	2013
Number of species detected	57	59	70	73	75	76
Models based on 5-min and 8-min counts converged	53 (93)	54 (92)	51 (73)	57 (78)	55 (73)	61 (80)
Models converged when based on 8-min but not 5-min counts	0 (0)	3 (5)	1 (1)	5 (7)	1 (1)	0 (0)
Models converged when based on 5-min but not 8-min counts	4 (7)	2 (3)	1 (1)	0 (0)	2 (3)	0 (0)
Neither model converged	0 (0)	0 (0)	17 (24)	11 (15)	17 (23)	15 (20)
$p \geq 0.3$ when based on 5-min and 8-min counts	31 (54)	28 (47) ^a	17 (24)	26 (36)	26 (35)	31 (41)
$p \geq 0.3$ when based on 8-min but not 5-min counts	4 (7)	4 (7)	4 (6)	4 (5)	2 (3)	4 (5)
$p \geq 0.3$ when based on 5-min but not 8-min counts	1 (2)	1 (2)	2 (3)	3 (4)	1 (1)	0 (0)
$p < 0.3$ when based on 5-min and 8-min counts	17 (30)	21 (36)	28 (40)	24 (33)	26 (35)	26 (34)

^a Blue-gray Gnatcatchers excluded because confidence intervals for occupancy ranged from zero to one.

Across ecosystems and years, point estimates of occupancy for $19 \pm 5\%$ of the species in a given ecosystem were 0.001–0.32 higher when based on 5-min than 8-min counts. This counterintuitive result reflects the manner in which occupancy is estimated. Occupancy estimates based on 5-min counts can be higher than those based on 8-min counts when naïve occupancy from 5-min and 8-min counts are similar, but the species is detected on fewer of the 5-min counts than the 8-min counts. Although the difference in occupancy estimates was slight, we suspect that it might be sufficient to affect estimates of species richness based on occupancy models (Iknayan et al. 2014), especially because sample sizes were too small to estimate occupancy for a substantial proportion of the avifauna in our ecosystems.

Hayes and Monfils (2015) suggested that point-count data are not well suited for occupancy modeling because the mobility of birds violates the closure assumption—the occupancy status of points does not change among counts. Because the area of most points is smaller than the smallest home range of the species sampled, individuals regularly move in and out of the points (Rota et al. 2009). Simulations indicated that even slight movements resulted in detection probabilities that were lower than the true value and occupancy estimates that were higher than the true value (Hayes and Monfils 2015). Our results were consistent with the results of these simulations. Ultimately, whether point-count data can be used to estimate occupancy hinges on the definition of use (i.e., open system) versus occupancy (i.e., closed system) (Latif et al. 2016).

Periodicity of sampling: trade-offs between single-day and multiple-days sampling

The results of this analysis provide knowledge that can facilitate effective, cost-efficient, and geographically transferable methods for sampling native anurans, birds, and butterflies. Inferences about trade-offs between single-day and multiple-days sampling generally were consistent among taxonomic groups and geographic regions despite substantial differences in biology among the taxonomic groups and ecology and land use among the regions. Additionally, these analyses provide evidence for evaluating whether the assumptions of occupancy theory are met in diverse taxonomic groups and ecosystems.

Birds. After removing species that were not detected during one of the two years, were not detected in a sufficient number of points, or for which models of detection probability did not converge, we were able to analyze data for 23 species in 2012 and 22 species in 2013. Occupancy estimates derived from the multiple-days design were higher than those derived from the single-day design for all species in 2012 (mean 0.17, range 0.04–0.33) and 2013 (mean 0.16, range 0.01–0.38). However, 95% confidence intervals from the multiple-days and single-day models overlapped for 20 species in 2012 and all species in 2013. Estimates of p^* were higher when based on data from the single-day design than from the multiple-days design for all species in 2012 (mean 0.14, range 0.01–0.39) and 21 species in 2013 (mean 0.11, range - 0.09–0.33). However, 95% confidence intervals around estimates of p^* based on the two sampling designs overlapped for 9 species in 2012 and 19 species in 2013.

There are at least two reasons why occupancy estimates based on the multiple-days design consistently were higher than those based on the single-day design. First, multiple-days estimates of detection probability were lower than the single-day estimates. As detection probability

decreases, detection-weighted occupancy estimates increase relative to naïve occupancy estimates. Second, the proportion of sites on which species were detected during at least one survey was higher when the multiple-days design was implemented than when the single-day design was implemented. These two differences in detection probability between the two sampling designs likely would be consistent in other regions and time periods.

Our results suggest that the closure assumption was violated in the multiple-days design. Our findings are consistent with those of Rota et al. (2009), who found that the closure assumption was violated for all 18 species of breeding songbirds that they surveyed over 8 days in deciduous forests in the eastern United States. The multiple-days and single-day designs may estimate different parameters in species with a high proportion of mobile individuals. Because the multiple-days design is more likely than the single-day design to sample both breeding and dispersing males, we suggest that it estimates the probability of use rather than of occupancy. The period of sampling in the single-day design is short, which suggests that this design has a relatively high probability of meeting the closure assumption. However, the single-day design is less likely than the multiple-days design to sample dispersing individuals or individuals that are not associated with a territory.

Butterflies. Analyses are ongoing.

Anurans. After removing species that did not meet our criteria for consistent detection, we were able to analyze two years of data for 5 species that breed early in the season, 7 species that breed during the middle of the season, and 4 species that breed late in the season. Some individual species breed over a relatively long period of time, and therefore were included in more than one analysis. Occupancy estimates derived from the multiple-days design were higher than those derived from the single-day design for all 16 species models in 2012 (mean 0.14, range 0.02–0.47) and 13 of 14 species in 2014 (mean 0.12, range = -0.007–0.35). However, 95% confidence intervals around estimates of occupancy overlapped in all cases.

Estimates of p^* were higher when based on data from the single-day design than from the multiple-days design in all cases (2012: mean 0.09, range = 0.0002–0.28; 2014: mean 0.14, range 0.002–0.66). However, 95% confidence intervals around estimates of p^* based on the two sampling designs overlapped for 7 species in 2012 and 8 species models in 2014.

Simulations. The extent to which availability affected estimates of occupancy and p^* differed between survey designs (Figure 9). Availability led to greater bias in occupancy estimates in the single-day than in the multiple-days design. Occupancy estimates based on the multiple-days were unbiased when availability was ≥ 0.4 , but occupancy estimates based on the single-day design were biased whenever availability was < 1.0 . By contrast, availability led to greater bias in estimates of p^* in the multiple-days design than in the single-day design. Estimates of p^* based on the single-day design were unbiased when availability was ≥ 0.2 , but estimates of p^* based on the multiple-days design were biased whenever availability was < 1.0 .

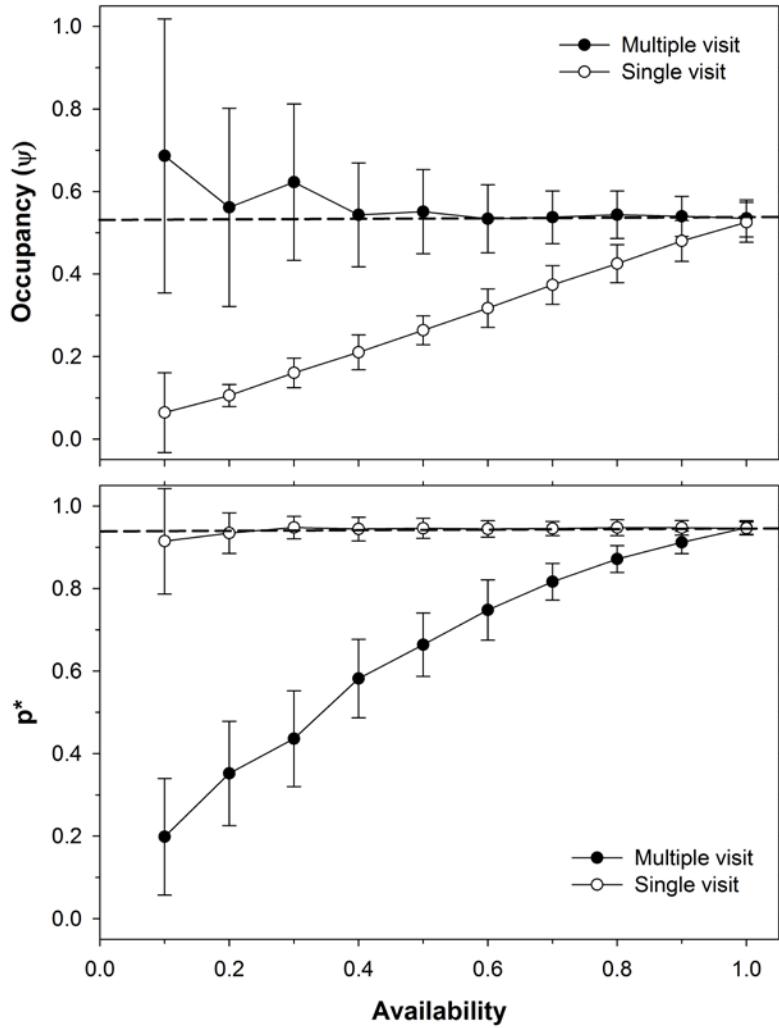


Figure 9. Simulation-based responses of estimates of occupancy and probability of detecting a given species at least once (p^*) to changes in availability of the species.

Although our work suggests that the closure assumption is met in the single-day design, this design potentially violates two other assumptions of occupancy models. First, it may violate the assumption of independent observations because an observer tends to remember species detected during previous surveys, particularly if the same observer conducts all surveys (MacKenzie et al 2006). Nevertheless, for nearly all species in our analyses, models that included an effect of previous detections on detection probability were not strongly supported. Second, the single-day design may introduce heterogeneity in detection probabilities among sites (MacKenzie et al. 2006) because different groups of sites are surveyed on different days, and environmental conditions may vary among days.

The precision of estimates of occupancy and detection probability that were based on the single-day design was higher than those based on the multiple-days design. Higher precision reflected a lower proportions of locations at which a species was observed during a subset of surveys. Increasing the number of surveys at a given site typically increases precision (MacKenzie and

Royle 2005), but there is a trade-off between the number of surveys conducted at a given site and the number of sites. In many ecosystems, the single-day design allows greater flexibility in allocation of the number of sites and surveys. All else being equal, precision of occupancy and detection estimates for common species will be maximized by conducting a greater number of surveys at fewer sites, and precision of estimates for rare species will be maximized by conducting fewer surveys at a greater number of sites (MacKenzie and Royle 2005).

Designing sampling to estimate occupancy requires consideration of the sampling effort available and trade-offs in allocation of that effort between numbers of sites and surveys (MacKenzie and Royle 2005). In most cases, less time is spent traveling between sites on a given day when the single-day design is implemented than when the multiple-days design is implemented (MacKenzie et al. 2006, Lele 2012). Because breeding birds cannot be sampled for more than four or five hours after sunrise, the single-day design generally allows one to sample a greater number of sites than the multiple-days design. We found that conducting three surveys of 131 sites within 14 parks with a multiple-days design required approximately twice as much time (214 hr) as did sampling with the single-day design (110 hr). These estimates did not include return-travel time, which did not limit sampling effort. As a result, we could visit more sites or conduct a greater number of surveys per site by implementing the single-day design. If the objective is to define habitat quality for birds, then we suggest implementing the multiple-days design because the estimates of occupancy derived from this design reflect habitat use (MacKenzie et al. 2006). If the objective is to monitor site or patch occupancy of birds, then we suggest implementing the single-day design because per-site sampling effort is lower and precision of occupancy estimates is higher than when the multiple-visit design is applied.

Estimation of species richness of multiple taxonomic groups on the basis of a single group

The results of this analysis provide knowledge that can facilitate effective, cost-efficient, and geographically transferable methods for assessing and monitoring species richness of native faunas and projecting responses of these taxonomic groups to land use and management. The methods that we developed can be applied to any taxonomic group in any location, although the extent to which indicator species are likely to be effective well may vary among taxonomic groups and locations. Additionally, these analyses provide evidence for evaluating theory on whether objectively selected subsets of a given taxonomic group support inference to species richness, whether currently or in other time periods or locations.

Our exploration of potential surrogates for estimation of species richness is novel in the extent to which we externally evaluated both spatial and temporal transferability. Our models were robust to the spatial and temporal variation in sampling locations that is relatively common in long-term data. Furthermore, we found that the predictive accuracy of models based on indicator species could exceed that of models based on environmental variables.

Point-level species richness of birds ranged from 1–22, and mean point-level species richness was greater in the western than in the central Great Basin (12.0 ± 3.5 [mean \pm SD] and 8.2 ± 3.6 , respectively). Similarly, mean annual species richness was greater in the western Great Basin (89.3 ± 4.9 from 2012–2014) than in the central Great Basin (81.0 ± 2.6 from 2012–2014). Mean

species richness of butterflies at a given transect in the central Great Basin was about twice that in the western Great Basin (21.6 ± 9.5 and 11.5 ± 7.2 , respectively), but mean annual species richness of butterflies was greater in the western (e.g., 82.3 ± 4.0 from 2013–2014) than in the central Great Basin (72.5 ± 3.5).

Explanatory ability of fitted models. Before confronting our models with independent data—data from locations or time periods that were not used to build the models—we evaluated the extent to which the models explained variation in observed species richness. Explained variation does not provide information on whether the model is likely to accurately predict species richness in those new locations or time periods. Fitted values of species richness that were based on both indicator species and environmental variables explained 0.27–0.69 of the variation in observed species richness of birds and 0.52–0.78 of the variation in observed species richness of butterflies (Table 2). Models that were based on same-taxon indicator species explained more variation than models that included cross-taxonomic indicator species. Apart from one case in which the explained variation was essentially equal, models that were based on both species and environmental variables explained 0.07–0.40 more variation in species richness than species-only models, and 0–0.23 more variation than models that were based on environmental variables only.

The accuracy of these predictions may be considerable statistically (Møller and Jennions 2002), but whether the predictions are sufficient to inform decision making depends on the particular situation (Runge et al. 2011, Keisler et al. 2013). It is possible that local managers or citizens more readily could be trained to sample a relatively small number of species than to sample all species in a fairly large taxonomic group. We strongly recommend external evaluation of any models that might be used to inform decision-making.

Table 2. Variation in species richness of birds or butterflies correctly explained by fitted random forest models that were based on indicator species and environmental variables (i.e., the fit of the random forest model to the data used for its construction). *Central* and *western* refer to subregions of the Great Basin. r^2 values are based on Pearson's r and were averaged across the ten iterations of each model. Full models included species and environmental variables.

Taxonomic group of response variable	Taxonomic group of indicator species	Subregion and years	r^2 , full model	r^2 , species-only model	r^2 , environmental variables-only model
birds	birds	western 2012–2014	0.50	0.32	0.43
birds	butterflies	western 2012–2014	0.39	0.09	0.39
birds	birds	central 2008–2010	0.57	0.48	0.46
birds	butterflies	central 2001–2003	0.27	0.20	0.07
birds	birds	central 2008–2014	0.69	0.70	0.56
birds	butterflies	central 2013–2014	0.55	0.15	0.55
birds	birds	western 2012	0.44	0.37	0.33
birds	butterflies	western 2012	0.30	0.07	0.30
butterflies	butterflies	western 2012–2015	0.78	0.64	0.68
butterflies	birds	western 2012–2014	0.73	0.38	0.73
butterflies	butterflies	central 1995–1997	0.78	0.67	0.55
butterflies	birds	central 2001–2003	0.52	0.18	0.42
butterflies	butterflies	central 2001–2014	0.71	0.53	0.61
butterflies	birds	central 1995–2014	0.54	0.31	0.49
butterflies	butterflies	western 2012–2013	0.73	0.56	0.62
butterflies	birds	western 2012	0.60	0.41	0.52

Fitted associations between species richness and environmental variables. Species richness of birds usually increased as canopy cover and the proportion of riparian cover increased, and decreased as riparian fragmentation increased (Table 3). The association between species richness of birds and canyon area was unimodal and concave (U-shaped). The shape of associations between species richness of birds and number of trees, terrain ruggedness, and minimum temperature varied noticeably between the central and western Great Basin. Species richness of butterflies generally increased as the maximum temperature decreased and as the abundance of nectar and mud increased. Species richness of butterflies also increased as the sampled area increased, and appeared to reach an asymptote in the western Great Basin. In the central Great Basin, species richness of butterflies increased as mean elevation decreased and as precipitation increased. In the western Great Basin, by contrast, species richness was greatest at intermediate values of elevation and precipitation.

Model evaluation. Consistent with our previous work, more variation in species richness of a given taxonomic group was predicted by same-taxon indicator species than by cross-taxonomic indicator species (Thomson et al. 2007). Much more variation in species richness of birds was predicted, whether in space or in time, by same-taxon indicator species than by cross-taxonomic indicator species (by an additional 0.12–0.40 in full models, and 0.32–0.51 in species-only models). The most accurate model, which was built with data from the central Great Basin and tested against data from a later time period in the same region, predicted 0.58 of the variation in species richness of birds. Whether the full model or species-only model predicted more variation in species richness was inconsistent, but differences between the two model types generally increased as the total variation explained decreased. Two of the environmental variables-only models predicted ≥ 0.25 of the variation in species richness of birds.

With one exception, same-taxon indicator species predicted more variation in species richness of butterflies than cross-taxonomic indicator species (0.15–0.61 more in full models, 0.08–0.68 in species-only models) (Table 2). However, occurrence patterns of birds predicted a maximum of 0.65 of the variation in species richness of butterflies, whereas occurrence patterns of butterflies predicted no more than 0.19 of the variation in species richness of birds. The most accurate model, which predicted 0.67 of the variation in species richness of butterflies in the western Great Basin in 2014, was built with data on environmental variables (Table 2). Four other environmental variables-only models predicted ≥ 0.25 of the variation in species richness of butterflies.

A possible explanation for the relatively poor predictions of species richness of birds from butterfly indicator species is that detection probabilities and occupancy of adult butterflies often increase as the abundance of nectar or mud increases (Fleishman et al. 2017), and in the Great Basin, these resources generally are most abundant in riparian areas with moderate canopy cover. Relatively few butterflies in the Great Basin occur in comparatively xeric shrublands or coniferous woodlands, which provide habitat for numerous species of birds.

In external evaluation, models based on same-taxon indicator species predicted more variation in species richness than those based on environmental variables in seven of eight cases.

Table 3. Variation in species richness of birds or butterflies correctly predicted by indicator species and environmental variables.

Central and *western* refer to subregions of the Great Basin (see text and Fig. 1). r^2 values are based on Pearson's r . Full models included species and environmental variables. Grey shading indicates models that predicted <0.25 of the variation in species richness.

Taxonomic group of response variable	Taxonomic group of indicator species	Subregion and years used to build the model	Subregion and years used to test predictions of the model	r^2 , full model	r^2 , species-only model	r^2 , environmental variables-only model
birds	birds	western 2012-2014	central 2012-2014	0.41	0.47	0.26
birds	butterflies	western 2012-2014	central 2013-2014	0.18	0.02	0.17
birds	birds	central 2008-2010	central 2012-2014	0.58	0.52	0.46
birds	butterflies	central 2001-2003	central 2013-2014	0.19	0.01	0.20
birds	birds	central 2008-2014	western 2012-2014	0.46	0.50	0.11
birds	butterflies	central 2013-2014	western 2012-2014	0.06	0.01	0.07
birds	birds	western 2012	western 2014	0.30	0.34	0.23
birds	butterflies	western 2012	western 2014	0.18	0.02	0.17
butterflies	butterflies	western 2012-2015	central 2013-2014	0.59	0.60	0.30
butterflies	birds	western 2012-2014	central 2013-2014	0.11	0.01	0.23
butterflies	butterflies	central 1995-1997	central 2013-2014	0.70	0.70	0.12
butterflies	birds	central 2001-2003	central 2013-2014	0.09	0.02	0.03
butterflies	butterflies	central 2001-2014	western 2012-2014	0.51	0.57	0.27
butterflies	birds	central 1995-2014	western 2012-2014	0.36	0.01	0.39
butterflies	butterflies	western 2012-2013	western 2015	0.53	0.48	0.46
butterflies	birds	western 2012	western 2014	0.65	0.40	0.67

Environmental variables-only models predicted 0.01–0.38 more variation than species-only models in the seven cases in which the latter predicted ≤ 0.02 variation in species richness. Thus, although there were instances in which the proportion of variation predicted by environmental variables was greater than the proportion predicted by indicator species, most of these models predicted relatively little variation in species richness in an absolute sense.

Identity and predictive capacity of indicator species. Thirty-four species of birds were included in ≥ 1 iteration of at least one of the four spatially transferable models of the species richness of birds (i.e., two full and two indicator-species only models). However, there was some consistency in the identity of the species included in multiple models. Dusky Flycatcher (*Empidonax oberholseri*), Mountain Chickadee (*Poecile gambeli*), Bushtit (*Psaltriparus minimus*), House Wren (*Troglodytes aedon*), American Robin (*Turdus migratorius*), Western Tanager (*Piranga ludoviciana*), and Cassin’s Finch (*Haemorhous cassinii*) were included in > 1 iteration of all of the spatially transferable models.

Thirty species of birds were included in ≥ 1 iteration of at least one of the four temporally transferable models of the species richness of birds. The indicator species included in the greatest proportion of models of the species richness of birds, all of which had positive associations with species richness, are fairly common and widespread in both the central and western Great Basin. Dusky Flycatchers are associated with riparian areas and adjacent vegetation; House Wrens with woodlands, often near edges; American Robins with woodland edges; and Cassin’s Finches in open, coniferous woodlands and in sagebrush (*Artemisia* spp.) steppe with scattered trees, often at relatively high elevations. Our models predict that the locations in which these four species co-occur (most of which are riparian) have relatively high species richness. Sage Thrasher and Sagebrush Sparrow (*Artemisiospiza nevadensis*), which had strong negative associations with species richness of birds, are associated with large sagebrush in areas with little tree cover. These species are most common in the valleys separating mountain ranges; we sampled relatively few locations in which they were likely to occur, and recorded few individuals.

Twenty-six species of butterflies were included in ≥ 1 iteration of at least one of the four spatially transferable models of the species richness of butterflies. As with birds, there was some consistency in the identity of species included in multiple models. Twenty-four species of butterflies were included in ≥ 1 iteration of at least one of the four temporally transferable models of the species richness of butterflies. Both of the butterfly species that were included in a high proportion of models of the species richness of butterflies are fairly widespread and conspicuous. *Icaricia lupini* occurs in diverse land-cover types. *Papilio rutulus* generally is associated with riparian areas, although it is quite vagile. *I. lupini* has multiple generations per season, whereas *P. rutulus* is univoltine and generally flies during the middle of the season.

Thirty-six species of birds were included in at least one of the two spatially and two temporally transferable models of the species richness of butterflies that explained ≥ 0.25 of the variation in the response variable. The bird species that had the strongest negative associations with species richness of butterflies typically occur in relatively dense woodlands or in shrub-dominated uplands, which generally are relatively late-successional and xeric communities with few sources of nectar. However, not all species with such land-cover associations had negative relations with species richness of butterflies. For example, Sage Thrasher (*Oreoscoptes montanus*), which had a

fairly strong positive association with species richness of butterflies, occurs in shrub-dominated uplands.

Strengths of association between species richness and the occurrence of butterfly indicator species generally were appreciably higher than those between species richness and the occurrence of bird indicator species.

Our work may suggest that tracking the occurrence of a subset of an assemblage during periods of environmental change will allow inference to species richness of the assemblage. However, given that adaptive phenotypic plasticity and evolution are species-specific (Ghalambor et al. 2007, Kinnison and Hariston 2007, Reed et al. 2011), current relations between indicator species and species richness likely are not stationary.

Use of occupancy as a surrogate measure of species richness: hierarchical models of occupancy

Analyses are ongoing. Results of the analyses will provide knowledge on the extent to which groups of birds with similar nesting habitat are likely to differ in their response to environmental change, and whether these differences are consistent among ecosystems. Results also will inform selection of environmental variables for inclusion in assessment and monitoring of species richness.

Preliminary results suggest that in the Chesapeake Bay Lowlands, occupancy of species that nest on the ground or in low shrubs is negatively associated with number of snag saplings and mean canopy height, whereas occupancy of the same group is positively associated with number of deciduous saplings and proportion of riparian cover. Persistence of species that nest on the ground or in low shrubs appears to be positively associated with proportion of mesic deciduous or mixed tree cover and proportion of conifer cover. Occupancy of species that nest in tall trees or shrubs was positively associated with structural heterogeneity, and persistence of this group was positively associated with proportion of developed land. The latter may reflect planting of large ornamental trees in many suburban areas. Occupancy of species that nest in tree cavities seems to be negatively associated with number of deciduous saplings (which are too small to support construction of a canopy nest) and positively associated with proportion of riparian cover.

Preliminary results suggest that detection probability of all groups in the western Great Basin is negatively associated with terrain ruggedness. Complex terrain may interfere with both spatial transmission of vocalizations and visual detection of birds. Occupancy of species that nest on the ground or in low shrubs may be negatively associated with riparian fragmentation and positively associated with elevation. Persistence of species that nest on the ground or in low shrubs seems to be lower in the Sierra Nevada than the Wassuk or Sweetwater Range, and colonization seems to be negatively associated with canopy prevalence. Occupancy of species that nest in tall trees or shrubs was positively associated with canopy prevalence. Persistence of the latter group was negatively associated with riparian fragmentation and positively associated with riparian cover and canopy prevalence. Occupancy of species that nest in tree cavities was negatively associated

with elevation and positively associated with terrain ruggedness, whereas persistence of the group was positively associated with canopy prevalence and elevation. Results from the central Great Basin are forthcoming.

Use of occupancy as a surrogate measure of species richness: estimation of the occupancy of butterflies in diverse biogeographic regions

Results of these analyses provide knowledge on the extent to which different species of butterflies may differ in their response to environmental change, and whether these differences are consistent among ecosystems. Our results also provide information to evaluate assumptions of occupancy theory.

Geographic variation in the extent to which assumptions of occupancy theory are met, and the manner in which such variation may be associated with regional differences in the biology of the focal species or taxonomic group, generally has not been addressed in the literature. Pursuing these areas of inquiry can inform the design of effective and cost-efficient assessment and monitoring. We found that the extent to which the closure assumption was met varied among ecosystems and years, and was greater in the Chesapeake Bay Lowlands than in the Great Basin. Geographic variation in the extent to which assumptions of occupancy theory are met, and the manner in which such variation may be associated with regional differences in the biology of the focal species. It is possible that the more-heterogeneous topography of the Great Basin mountain ranges in which we worked leads to greater variation in emergence dates and to more-extensive movements of individuals (e.g., because air flow along the elevational gradient can be strong) than in the relatively flat Chesapeake Bay Lowlands. Additionally, 85% of the species we modeled in the Chesapeake Bay Lowlands always or sometimes have more than one brood per year (thus would be available for sampling more consistently, and may be more amendable to occupancy modeling than species with one brood per year), compared to 20% and 33% of the species in the central and western Great Basin, respectively.

In each ecosystem, associations between one or more covariates and p_{ij} or ψ_i for at least one-third of the species—a total of 25 species-by-year models across the three ecosystems—either could not be estimated or seemed implausibly large (i.e., $\geq |10|$). Examination of the raw data allowed us to identify potential causes of the estimation problems for about 2/3 of these models. In most cases, problems appeared to stem from clustering of detections at one end of the gradient of values of a covariate. For example, precipitation values for the transects in the western Great Basin on which *S. zerene* was detected in 2014 generally were relatively high. In a few cases, naïve occupancy may have been too low (e.g., 0.35) or too high (e.g., 0.66) to allow estimation of parameters.

Chesapeake Bay Lowlands. Maximum single-year estimates of detection probabilities (p_{ij}) ranged from 0.14 to 0.74. Nectar was associated with p_{ij} of nine species in one of two years and three species in both years. In all but one case, as the abundance of nectar increased, p_{ij} increased. Occupancy (ψ_i) ranged from 0.28 to 0.89. We identified covariates associated with ψ_i of five species in one year and eight species in two years. In the latter cases, one or more of the same covariates was associated with ψ_i of five of the species in both years. The deciduous

proportion of the basal area of trees was associated with ψ_i of nine species in 2013 and six species in 2014. Occupancy of one species in 2013 and five species in 2014 was associated with the number of deciduous stems. Structural heterogeneity was associated with ψ_i of four species in 2013 and two species in 2014. Edge length was associated with ψ_i of one species each in 2013 and 2014. In 2013, the interaction between edge length and structural heterogeneity was associated with ψ_i of one species.

In part, the association between occupancy and either structural heterogeneity or the dominance or abundance of deciduous woody species may reflect that the larval host plants of five of the species we modeled are deciduous. Additionally, structural heterogeneity may be a surrogate measure of intensity of browsing by white-tailed deer. Areas in which white-tailed deer are abundant tend to have relatively little understory, thus relatively few grasses or forbs that serve as larval host plants or nectar sources. Removal of the understory also changes microclimate and may expose immature life stages to higher probabilities of predation.

Central Great Basin. Maximum single-year p_{ij} ranged from 0.28 to 0.97. Abundance of nectar was associated with p_{ij} of three species in 2013 only, two species in 2014 only, and two species in both years. Abundance of mud was associated with p_{ij} of two species in 2013 only, one species in 2014 only, and six species in both years. Detection probability increased as abundance of nectar or mud increased in all but one case. Single-year ψ_i ranged from 0.44 to 0.98. Regression coefficients could not be estimated or were $\geq |10|$ for one species in 1995 and two species each in 2013 and 2014. In all other cases, one or more covariates were associated with ψ_i of all species in each year. Occupancy of two species was associated with elevation only. At least some of the covariates that were associated with ψ_i of the other species varied among years. Elevation (whether as a linear or a quadratic function) was associated with ψ_i of six species in 1995, 11 species in 2013, and 13 species in 2014. Occupancy of six species in 2013 and five species in 2014 was associated with mud abundance. Precipitation was associated with ψ_i of seven species in 1995 and three species in each of 2013 and 2014. Nectar abundance was associated with ψ_i of four species in 2013 and five in 2014. Occupancy of three species in 1995, four in 2013, and three in 2014 was associated with terrain ruggedness.

Western Great Basin. Maximum single-year p_{ij} for a given species ranged from 0.34 to 0.99. Abundance of nectar was associated with p_{ij} of two species in 2014 only and four species in both 2013 and 2014. Abundance of mud was associated with p_{ij} of four species in 2013 only, two in 2014 only, and three in both years. Single-year ψ_i ranged from 0.31 to 0.78. Regression coefficients and effect sizes could not be estimated or were $\geq |10|$ for one species each in 2013 and 2014. In all other cases, one or more covariates were associated with ψ_i of all species in both years. A single covariate—elevation or precipitation—was associated with ψ_i of three species in both 2013 and 2014. At least some of the covariates that were associated with ψ_i of the other species varied between years. Elevation (whether as a linear or a quadratic function) was associated with ψ_i of nine species in 2013 and six species in 2014. Precipitation was associated with ψ_i of eight species in 2013 and seven in 2014. Occupancy of five species in either year was associated with terrain ruggedness. Mud abundance was associated with ψ_i of one species in 2013 and one species in both years. Nectar abundance was associated with ψ_i of two species in 2014.

Either elevation or precipitation were associated with occupancy of all species in the central and western Great Basin. Strong relations between elevation and occupancy were consistent with previous work in these ecosystems (e.g., Fleishman et al. 1998, 1999, 2001a, b). In the central Great Basin, about twice as many associations between occupancy and precipitation were observed in 1995, a water year with unusually high precipitation, than in 2013 or 2014. The direction of the associations between occupancy and precipitation was inconsistent among species. Although extreme winters can increase mortality of overwintering life stages, especially larvae (Douglas 1986, Dennis 1993), precipitation may forestall senescence of host plants and nectar sources.

Our estimates of abundance of nectar and mud were coarse; they were intended to be rapid and fairly repeatable among observers. Nevertheless, p_{ij} in one or more years was associated with abundance of nectar or mud for 92% of the species in the Chesapeake Bay Lowlands, all of the species in the central Great Basin, and 93% of the species in the western Great Basin. In almost all cases, p_{ij} increased as the abundance of these resources increased. These relations are consistent with field experience. For example, species in the Papilionidae and Polyommatinae often are detected at mud. However, to the best of our knowledge, these relations have not previously been quantified at the assemblage level. Detection probabilities tended to be relatively high for species that are abundant, have limited vagility and circumscribed habitat, or are conspicuous. Detection probability tended to be associated more consistently than occupancy with abundance of nectar or mud. Continuous estimates of sugar mass may be more closely associated with occupancy than categorical abundance of nectar (Pavlik et al. in review).

We modeled seven species that occurred in both the central and western Great Basin, but covariates associated with p_{ij} and ψ_i of those species, or the direction of association with the same covariate, often differed among ecosystems. This variation may reflect that our study locations in the central and western Great Basin are within different centers of differentiation or zoogeographic regions (Austin and Murphy 1987). In many cases, different subspecies occupy the two regions, and their local ecology may be sufficiently distinct to affect covariate associations.

Occupancy rarely has been estimated for a high proportion of the species within an assemblage of butterflies, and our work highlighted some of the applications in which occupancy estimation has limitations. Single-species occupancy models often are applied to many species that were sampled simultaneously. These situations may require or lead to the assumption that sampling of each modeled species was sufficiently and equally robust. But given typical financial and logistical constraints, it rarely is tractable to sample an assemblage, especially one that is highly dynamic, with a design that is ideal for estimating occupancy of the majority of individual species. For example, assemblage-level surveys generally encompass areas that are unlikely to be occupied by a given species, which may complicate parameter estimation. Moreover, if organisms are sufficiently mobile that the occupancy status of fairly small sites is likely to change between surveys, as is the case with adult butterflies, inferences about the environmental variables that are associated with p_{ij} and ψ_i may become biased (e.g., Hayes and Monfils 2015). Our work both elucidates trade-offs among application of occupancy models to multiple co-occurring species of butterflies and highlights a number of novel ecological relations, especially the extent to which detection probabilities may relate to ephemeral resources.

Use of occupancy as a surrogate measure of species richness: environmental associations with multiple states of anuran occupancy

Results of this ongoing analysis improve understanding of assessment and monitoring of anurans at multiple spatial and temporal scales and provide information for projecting responses of anurans to environmental change. We first applied multiple-state models to anurans because the methods were highly consistent with the manner in which anuran data were collected—a categorical calling index rather than an estimated count (number of animals). Given that our application to date generally has met technical criteria for success (e.g., most models converged and variances were not extreme) and yielded useful biological inferences, we believe there is considerable potential to develop abundance classes for birds and butterflies and apply the models to additional data collected as part of the current project.

We detected Fowler's toads, Cope's gray tree frogs, and spring peepers at 64, 73, and 71 of 108 wetlands, respectively. The calling index of Fowler's toads, Cope's gray tree frogs, and spring peepers was high during ≥ 1 survey at 26, 41, and 49 wetlands, respectively.

Estimates of detection probability for anurans at low abundance in a single year ranged from 0.01 ± 0.04 (SE) (Fowler's toad, 2015) to 0.90 ± 0.05 (spring peeper, 2013) (Table 5). Estimates of detection probability for anurans at high abundance in a single year ranged from 0.23 ± 0.04 (Fowler's toad, 2015) to 1.0 (spring peeper, 2012 and 2013). Multiple-year estimates of occupancy at low abundance fell between 0.51 ± 0.07 (spring peeper) and 0.80 ± 0.06 (Fowler's toad), whereas estimates of occupancy at high abundance fell between 0.40 ± 0.10 (Fowler's toad) and 0.92 ± 0.05 (spring peeper). The probability of any of the species colonizing a previously vacant wetland, whether in a low or a high abundance state, did not exceed 0.12 (Table 5), whereas the probability of extirpation, remaining at low abundance, or transitioning from high to low abundance was a minimum of 0.80. The probability of remaining at high abundance fell between 0.18 ± 0.09 (Cope's grey tree frog) and 0.48 ± 0.10 (Fowler's toad).

Although scale is referenced often in ecology, models that include covariates measured at multiple extents are relatively uncommon. Occupancy of pond-breeding anurans was associated with variables at multiple spatial extents that are relevant to different stages of their life history. The association between occupancy and environmental variables at the smallest extent, which corresponded to breeding, was poor to fair (AUC 0.60–0.75), and was equal or weaker than associations between occupancy and environmental variables at extents that corresponded to migration (AUC 0.70–0.84) and dispersal (AUC 0.64–0.74). Models that included covariates at multiple extents generally explained more variation in occupancy than models that included covariates at one extent (AUC 0.71–0.92).

Both single-state and multiple-state models of occupancy of Fowler's toads suggested that occupancy was strongly associated with the magnitude of forest aggregation within 400 m of the wetland (positive), the percentage of upland forest cover within 400 m (positive), the density of highways with high traffic volume within 4 km (negative), effective mesh size within 1.5 km (positive), the percentage of wetland cover within 3.5 km (positive), and the percentage of impervious surface within 2.5 km (negative). Percentage of canopy may serve as a proxy measure of shoreline vegetation structure.

Table 5. Preliminary results of multiple-season, multiple-state analyses of the occupancy of anurans in the Chesapeake Bay Lowlands. Psi, occupancy. State 1, low abundance; state 2= high abundance. SE, standard error.

	Spring peeper		Cope's grey tree frog		Fowler's toad	
Estimate	Estimate	SE	Estimate	SE	Estimate	SE
Occupancy, low abundance	0.51	0.07	0.64	0.07	0.80	0.06
Transition from absent to low abundance	0.01	0.01	0.12	0.05	0	NA
Remain at low abundance	0.92	0.06	0.90	0.07	1.0	NA
Transition from low abundance to absent	1.0	NA	1.0	NA	0.94	0.04
Occupancy, high abundance	0.92	0.05	0.75	0.11	0.40	0.10
Transition from absent to high abundance	0	0	0.09	0.20	0	0
Remain at high abundance	0.45	0.11	0.18	0.09	0.48	0.10
Transition from high to low abundance	0.82	0.64	0.80	0.07	0.93	0.06
Detection probability, low abundance, 2011	0.49	0.21	0.35	0.09	0.06	0.02
Detection probability, low abundance, 2012	0.27	0.16	0.13	0.05	0.11	0.04
Detection probability, low abundance, 2013	0.90	0.05	0.17	0.06	NA	NA
Detection probability, low abundance, 2014	0.66	0.13	0.10	0.03	0.08	0.05
Detection probability, low abundance, 2015	0.48	0.15	0.24	0.06	0.01	0.04
Detection probability, high abundance, 2011	0.97	0.02	0.47	0.04	0.39	0.07
Detection probability, high abundance, 2012	1.0	0	0.41	0.06	0.30	0.04
Detection probability, high abundance, 2013	1.0	0	0.58	0.04	0.38	0.04
Detection probability, high abundance, 2014	0.96	0.02	0.47	0.08	0.34	0.04
Detection probability, high abundance, 2015	0.97	0.02	0.54	0.05	0.23	0.04

Both single-state and multiple-state models of occupancy of Cope's gray tree frogs suggested that occupancy was strongly associated with whether the wetland was open water or had emergent vegetation, the percentage of upland forest cover within 1 km (positive), the magnitude of forest aggregation within 1 km (positive), the percentage of impervious surface within 3.5 km, the density of highways with high traffic volume within 500 m (negative), effective mesh size within 5 km (positive), and the percentage of wetland cover within 5 km. The species was more strongly associated with wetlands than with ponds.

Both single-state and multiple-state models of occupancy of spring peepers suggested that occupancy was strongly associated with the percentage of canopy cover around a wetland (positive), the magnitude of forest aggregation and the percentage of forest cover within 600 m (positive), the percentage of impervious surface within 4.5 km (negative), effective mesh size within 1.5 km or 4.5 km (positive), and wetland density within 3.5 km (positive). The single-state analysis suggested that occupancy was positively associated with the length of the perimeter of the wetland, whereas the multiple-state analysis suggested that occupancy was associated with wetland area (positive) and highway density within 5 km (negative).

Many anuran populations are believed to function as metapopulations (Smith and Green 2005). Although the process of anuran dispersal is poorly understood (Semlitsch 2008), occupancy is negatively related to urbanization (Rubbo and Kiesecker 2005), roads (Eigenbrod et al. 2008), and distance to neighboring wetlands (Scherer et al. 2012). The distance at which many of the migration-level and dispersal-level covariates were associated with occupancy was the maximum quantified, suggesting that dispersal may be occurring across areas larger than we defined.

Our preliminary results suggest that populations of Fowler's toads, Cope's gray tree frogs, and spring peepers in the Chesapeake Bay Lowlands generally are stable, but if these anurans are extirpated from wetlands in the region, the wetlands are unlikely to be recolonized.

Responses of songbird occupancy to environmental change

Results of this analysis provide information that facilitates projection of the effects of land use and management actions on native birds in the Chesapeake Bay Lowlands. Although urbanization is likely to continue throughout the ecosystem, densities of white-tailed deer can be managed via culling.

To the best of our knowledge, we conducted the first statistically rigorous, multiple-year investigation of regional relations between intensity of deer browsing and densities of individual species and guilds of birds. Our results were consistent with a growing body of evidence that deer affect the quality of habitat for birds, especially woodland songbirds that depend on foliage below the browse line (e.g., McShea and Rappole 2000, Cardinal et al. 2012). Areas in which densities of deer are high have little vegetation cover below the browse line (Martin et al. 2010), and direct predation of songbird nests by deer has been documented (Luepold et al. 2015).

We estimated detection probability as a nuisance parameter to adjust pellet and bird densities. The probability of detecting deer pellets was significantly lower in coastal Virginia than inland

Virginia. All detection probabilities of individual species and guilds of birds were ≤ 0.34 . Detection probabilities at the guild level and at the level of species within that guild did not differ in coastal Virginia. The probability of detecting species that nest in understory shrubs and glean understory foliage did not differ between regions. However, the probability of detecting the other two guilds was lower in inland than coastal Virginia.

Relatively high intensity of deer use in coastal Virginia was correlated with substantial levels of local forest fragmentation, which is associated with high-quality deer habitat. The mean extent of forest-road, forest-grassland, forest-row crop, and forest-rural edges was 232%, 346%, 176%, and 252% higher, respectively, in coastal Virginia than inland Virginia. Deer use in 2012 was greater in coastal Virginia (2014 pellets ha^{-1} , range 0–28,193 ha^{-1}) than inland Virginia (0 pellets ha^{-1} , range 0–19,600 pellets ha^{-1}) ($W = 5,462, P = 0.01$). We detected no pellets in 38% of the sites in coastal Virginia and 57% of the sites in inland Virginia. The mean number of deer harvested in coastal Virginia from 2004–2013 (4.73, CI 4.45–5.00) was greater than in inland Virginia (2.99, CI 2.79–3.19) ($t_9 = 11.1, P < 0.001$).

Deer use and the density of shrub-nesting foliage gleaners in coastal Virginia was negatively correlated ($r_s = -0.35, P < 0.01$) (Figure 10). In coastal Virginia, deer use and the density of canopy-nesting or cavity-nesting species that feed in the canopy or sally aerially was positively correlated ($r_s = 0.27, P = 0.03$). Deer use and the density of guilds in inland Virginia was not significantly correlated. In coastal Virginia, deer use was negatively correlated with the density of White-eyed Vireos (*Vireo griseus*), Red-eyed Vireos (*Vireo olivaceus*), Black-and-white Warblers (*Mniotilla varia*), Hooded Warblers (*Setophaga citrina*), Prairie Warblers (*Setophaga discolor*), and Scarlet Tanagers (*Piranga olivacea*). Prairie Warblers, which breed in forests with open canopy and shrubby undergrowth (Nolan et al. 1999), are classified as a species of highest conservation concern at the continental level by Partners in Flight (Rosenberg et al. 2016). Local populations of Hooded Warblers, which nest in understory shrubs, have declined considerably as the shrub layer has disappeared (Chiver et al. 2011).

Deer use was positively correlated with the density of Eastern Wood-Pewees (*Contopus virens*), Acadian Flycatchers (*Empidonax virescens*), Blue Jays (*Cyanocitta cristata*), Carolina Chickadees (*Poecile carolinensis*), and White-breasted Nuthatches (*Sitta carolinensis*). Some of these correlations may reflect overlap in the distribution of habitat quality for deer and some species of birds. For example, both Carolina Chickadees and deer thrive in wooded suburbs (Mostrom et al. 2002).

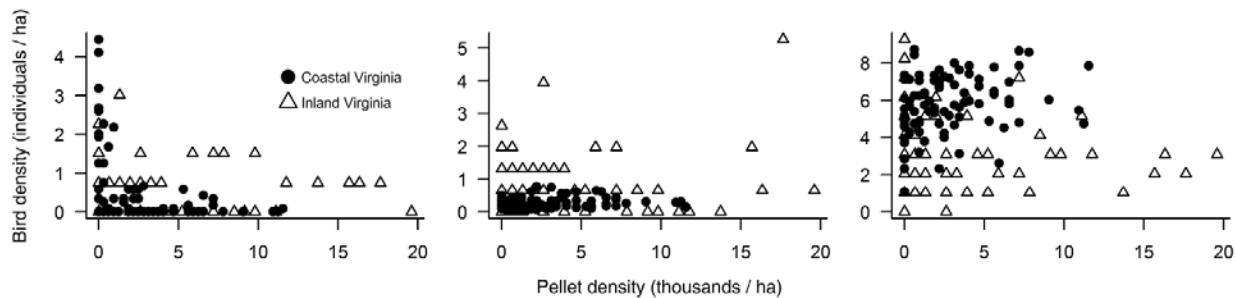


Figure 10. Relations between density of birds in different guilds and relative intensity of deer use (density of deer pellets). Left, shrub-nesting foliage gleaners; middle, species that nest in the canopy and feed on open ground; right, middle, canopy-nesting or cavity-nesting species that feed in the canopy or sally aerially.

Partitioning drivers of beta diversity

Results of this analysis may increase the ability to develop effective and cost-efficient methods for assessing and monitoring native birds and butterflies in multiple subregions of the Great Basin across space and time. Assessment and monitoring of native faunas is likely to become increasingly relevant if removal of conifers, intended to increase habitat quality for Greater Sage-Grouse, is implemented as planned.

Temporal patterns. Our preliminary results indicated that bird species' identities were more consistent through time than would be expected under a null model, which suggests that distributions, although variable, are associated with abiotic or biotic environmental attributes. More variation in beta diversity was attributable to turnover than to nestedness—increases in species richness do not simply represent addition of species to a core group. However, observed nestedness was generally higher than under a null model, which is consistent with the fact that the species pool is relatively similar across the region.

Temporal patterns in turnover and nestedness of butterfly assemblages were similar to those of bird assemblages: turnover was lower than expected and nestedness higher than expected under a null model. Levels of nestedness of butterflies were equal to or greater than those of birds, whereas turnover was lower.

Little of the variation in temporal turnover and nestedness was explained by zoogeographic region or spatial resolution, although several weak associations were apparent. Temporal turnover and nestedness of bird assemblages were higher in the central Great Basin than in the western Great Basin, and at the level of points than at the level of canyons. Turnover of butterfly assemblages was lower in the central Great Basin than in the western Great Basin, but did not differ among spatial resolutions. The level of nestedness of butterfly assemblages did not differ between regions or spatial resolutions.

Spatial patterns. Bird species' identities again were more consistent in space than would be expected under a null model, and were more consistent among canyons within mountain ranges than among points within canyons. Spatial nestedness in bird assemblages was often higher than expected under a null model, and was lower in the western than in the central Great Basin. The majority of spatial variation in bird assemblages was due to turnover rather than nestedness.

Spatial turnover in butterfly assemblages was often lower than expected under a null model, and was higher in the western than in the central Great Basin. This may reflect that there is more biogeographic differentiation in our western Great Basin study areas than in our study areas in the central Great Basin. The avifauna of the east slope of the Sierra Nevada includes several species that typically do not occur further east in the Great Basin, and vice versa. Spatial

turnover was lower in butterfly assemblages than in bird assemblages. Spatial nestedness in butterfly assemblages often was higher than in bird assemblages. The latter is consistent with the fact that although butterflies have fairly specific habitat requirements as larvae, their adult habitat requirements may be more similar than that of birds.

Conclusions and Future Research and Implementation

We achieved the objectives of the statement of need to which the project responded by providing knowledge that improves understanding of assessment, monitoring, and management of diverse native species at multiple spatial and temporal scales. This knowledge and understanding can directly inform development of effective and cost-efficient methods for assessment, monitoring, and projection of the effects of land use and management actions. We empirically tested diverse aspects of theory related to assessment and monitoring of native species, including the fact that habitat is species-specific, and therefore different species will have different responses to environmental change. Our work provides information on the extent to which theory is applicable to multiple taxonomic groups that often are the focus of assessment and monitoring, and how such applicability varies within extensive ecosystems and among ecosystems.

In some cases, we met the project objectives in ways that were different from what we initially expected. For example, we anticipated that we would incorporate estimates of occupancy into our analyses of the explanatory and predictive ability of indicator-species models. However, we discovered through analyses of birds and butterflies that because detection probabilities for many species were below 0.3, we often could not estimate occupancy for more than 50% of the species detected in each ecosystem and year. As a consequence, our response variable in hierarchical modeling of species richness, indicator species, and beta diversity was naïve occupancy rather than detection-weighted occupancy. These results provide empirical evidence that some applications of occupancy models that have been suggested in the literature may not be effective in practice, especially for organisms with relatively dynamic short-term distributions or in ecosystems in which weather and climate are relatively variable and unpredictable.

Extents of sampling and management

Hierarchical estimates of species richness and analyses of beta diversity highlighted differences in the spatial extent at which birds and butterflies appear to respond to their environment. In the mountains of the Great Basin, canyons appear to be a more biogeographically meaningful spatial unit for birds than relatively small points that typically are used as sampling units for that taxonomic group. Therefore, it may be worthwhile to sample birds in multiple locations in a given canyon, and to include canyon as a covariate in analyses, rather than treating points as replicates independent of the canyon within which they are embedded.

In our hierarchical analyses of species richness, the proportion of variance in canyon-level cumulative species richness of birds that we were able to explain as a function of environmental covariates was at least double the proportion we could explain at the point level in both the central and western Great Basin. Moreover, a combination of canyon-level and point-level processes explained more variation in cumulative species richness of birds than did point-level processes alone. These results suggest that the effects of land use or management in one area of a canyon, especially if related to riparian areas, may have indirect effects on birds that breed throughout the canyon.

By contrast, hierarchical analyses of species richness allowed us to explain more than 0.70 of the transect-level variation in cumulative species richness of butterflies in both the central and western Great Basin. Similarly, in analyses of beta diversity in the central and western Great Basin, temporal turnover and nestedness of bird assemblages was greater at the level of points than the level of canyons, whereas temporal beta diversity of butterflies did not differ between spatial resolutions. These results suggest that management of butterfly habitat may be effective at relatively small extents, whereas management of bird habitat may need to be undertaken at larger extents.

The extent to which processes at multiple extents are associated with local occupancy also was apparent in preliminary results from multiple-state models of anuran occupancy. Although many populations appeared to be stable, we found little evidence of colonization by anurans, which suggests that if anurans are extirpated from a given natural or anthropogenic wetland in the Chesapeake Bay Lowlands, that location is unlikely to be recolonized.

Estimation of occupancy versus species richness

We noted above that although the difference in estimates of bird occupancy that were based on 5-min and 8-min counts in the Chesapeake Bay Lowlands and central and western Great Basin was slight, it might be sufficient to affect estimates of species richness of birds that are based on occupancy models (Iknayan et al. 2014), especially because sample sizes were too small to estimate occupancy for a substantial proportion of the avifauna. We conducted a simple test of the effects of count duration on naïve estimates of species richness of birds (i.e., simple counts not standardized by area to which sampling was extrapolated, number of individuals sampled, or detection probability) at nested spatial extents. This relation has been examined in many studies, but evidence is equivocal and likely reflects variation among land-cover types (Petit et al. 1995, Shiu and Lee 2003), ecosystems, sampling designs, and analysis methods. The number of species detected increases as count duration increases, sometimes substantially even at 1 min increments (Thompson and Schwalbach 1995), but perhaps less so when estimates of species richness are based on multiple counts throughout the season rather than one count (Buskirk and McDonald 1995). In general, it is not uncommon for ca. 65–90% of detections of a given species (Reidy et al. 2011), of all species (Tegler-Amones et al. 2012), or of the estimated mean number of species to be recorded within the first 5 min of a count (Esquivel and Peris 2008). By contrast, the percentage of mean deviance explained by generalized additive models of distributions of bird species in southwestern France that were based on either 5 min or 10 min counts was the same (25%); increasing the duration to 20 min increased the mean deviance explained to 28% (Bonthoux and Balent 2012). We aimed not only to better understand sampling trade-offs in our own study systems but to contribute to ongoing, rigorous assessments of field methods, including methods associated with counts of organisms.

We calculated species richness (number of species counted, not weighted by detection probability) of birds in 2012 and 2013 at the level of points. In the western and central Great Basin we also calculated species richness at two nested levels: canyons or polygons defined by previous or planned management treatments, and mountain ranges. Where species richness estimated on the basis of 5 min and 8 min counts differed, we identified the additional species

that were detected from 5–8 min. We compared mean species richness at the level of points in the Chesapeake Bay Lowlands and central and western Great Basin, and at the level of canyons in the central and western Great Basin, with one-tailed paired *t*-tests in StatPlus (v.5.8, AnalystSoft, Alexandria, Virginia). We used counts for this comparison because the proportion of species for which sample sizes were insufficient to model occupancy was high.

Data were sufficient to estimate occupancy for 26 of the 62 species in the Chesapeake Bay Lowlands. Data were sufficient to estimate occupancy for 18 of the 79 species detected in the central Great Basin in 2012 (23%) and 26 of the 80 species detected in 2013 (33%). We estimated occupancy for 25 of the 87 species detected in the western Great Basin in 2012 (29%) and 29 of the 86 species detected in 2013 (34%).

In all three ecosystems, both point-level and canyon-level estimates of species richness based on 8 min counts consistently were higher than those based on 5 min counts, and all differences were statistically significant (Table 4). There was no clear pattern in the identity or attributes of species that were detected from 5–8 min in a given location or year.

Table 4. Naïve estimates of species richness of birds at the point level and, in the central and western Great Basin, at the canyon level on the basis of points sampled for 5 and 8 min. All tests statistically significant ($p < 0.001$). SD, standard deviation.

		mean	SD	df	<i>t</i>
Point level					
Chesapeake Bay Lowlands					
2012	5 min	13.82	3.10	130	18.65
	8 min	15.92	3.31		
2013	5 min	13.68	3.14	130	15.84
	8 min	15.61	3.47		
central Great Basin					
2012	5 min	7.08	3.18	295	16.89
	8 min	8.23	3.63		
2013	5 min	7.88	3.24	313	17.82
	8 min	9.08	3.71		
western Great Basin					
2012	5 min	10.08	3.05	157	15.30
	8 min	11.64	3.48		
2013	5 min	10.44	3.11	157	15.35
	8 min	11.89	3.35		
Canyon level					
central Great Basin					
2012	5 min	24.59	7.68	26	6.91

	8 min	26.81	8.58		
2013	5 min	25.28	8.04	28	9.44
	8 min	27.69	8.29		
western Great Basin					
2012	5 min	31.77	6.37	12	5.59
	8 min	34.54	5.92		
2013	5 min	33.08	5.53	12	5.84
	8 min	35.00	5.34		

Inferences from occupancy models

The primary focus of our occupancy models was elucidating species-environment relations rather than precise estimation of occupancy per se. In that context, if one must decide between increasing the number of sample units or increasing the number of visits, we believe that increasing the number of sample units remains more effective. Additionally, estimation of use may be equally or more informative than estimation of occupancy for exploring species-environment relations. Given that few if any of our systems appear to have been closed, it is likely that our models largely estimated use.

Our mechanistic research on Wood Thrushes (*Hylocichla mustelina*) in the Chesapeake Bay Lowlands (Jirinec et al. 2016) highlighted the extent to which the availability of species for sampling is likely to change within a season, even for species that are territorial. Jirinec et al. (2016) tracked 37 radio-tagged males and used the resulting data to construct 95% kernel diurnal home ranges. They also tagged and tracked the female mates in 10 home ranges. Of 74 male night roosts, 31% were located outside diurnal home ranges.

Our work highlighted the extent to which abundance of nectar and mud may be associated with detection probabilities and occupancy or use of butterflies. Nectar and mud generally have been underemphasized in assessment and monitoring programs for butterflies, whereas more emphasis has been placed on larval hostplants. Previous laboratory and controlled experiments demonstrated that some species of butterflies may prefer sucrose to other sugars. However, sugar use has not been quantified for an assemblage of butterflies in the field. The abundance of nectar-producing plants, and the volume and concentration of the nectar in those plants, may peak in the initial years following a major disturbance such as fire, facilitating investigation of nectar use by butterflies. In 2014 and 2015, we surveyed butterflies and vegetation within the boundary of the Rim Fire (Stanislaus National Forest, Tuolumne County, California), a major fire that occurred in 2013. We quantified the masses of glucose, fructose, and sucrose for all plant species on which we observed butterflies feeding. We tested whether intensity of use of each 20 nectar sources (the number of butterflies observed taking nectar from each source across both years) was associated with the total sugar mass, mass of sucrose, or relative proportion of sucrose. We found no evidence that intensity of butterfly use was associated with sugar mass, mass of sucrose, or the relative proportion of sucrose (Pavlik et al. unpublished manuscript). Instead, butterflies appeared to use indiscriminately any nectar sources that were available to them. The difference between apparent sugar preferences in the laboratory and in the field may

be explained in part by resource availability, and may change as vegetation succession progresses.

Our work allowed us to draw inference to how species richness and occupancy of birds may respond to environmental changes in the Chesapeake Bay Lowlands and central and western Great Basin that largely can be controlled by management. For example, we were able to gauge the extent to which given levels of fragmentation of deciduous forest in the Chesapeake Bay Lowlands, and given densities of white-tailed deer, may positively or negatively affect density of individual species and functional groups of songbirds, including species that are declining across the region. Ongoing analyses of responses of functional groups of birds in the Great Basin to differences in vegetation structure and composition will provide information on how species that primarily are associated with shrublands, coniferous woodlands, and adjacent riparian areas may respond to planned removal of native pinyon (*Pinus monophylla*) and juniper (primarily *Juniperus osteosperma* and *J. occidentalis*) trees on as many as 120,000 km² (30 million acres).

Future research

We think there is considerable potential to conduct novel, empirical tests of hypotheses about the information content of occupancy estimates. As noted above, theory suggests that occupancy is a reliable surrogate measure of a species' abundance and that abundance, in turn, is strongly related to probability of persistence. However, empirical tests of the hypothesized relations between measures of occurrence and persistence have not been conducted. We suggest that it would be valuable and feasible to test whether occupancy, density (abundance per unit area), and reproductive success are correlated. Given that maximizing the probability of species persistence commonly is a high priority for resource managers, this work would be greatly relevant to decision-making. Additionally, theory suggests that environmental covariates that explain considerable variation in observed occupancy may be interpreted as measures of habitat quality, and used to project occupancy in unsampled locations or time periods. Testing this hypothesis would be relevant to management because measurement of environmental variables typically is more feasible than measuring occupancy or demography, and measures of environmental variables often have less uncertainty than measures of the distribution, survival, or reproduction of individual animals. In the Chesapeake Bay Lowlands, results would be highly relevant to management of populations of white-tailed deer, which have substantial effects on plant and bird communities. In any part of the Great Basin, our results would be applicable to planned management treatments on public lands, such as removal of conifers that is intended to increase the probability of persistence of Greater Sage-Grouse (*Centrocercus urophasianus*) and benefit more than 350 other species of animals (BLM 2015, USFS 2015).

We initially used data on birds and butterflies from the central and western Great Basin to estimate species richness of multiple taxonomic groups on the basis of a single group. We used these data because they best supported external evaluation of the spatial and temporal transferability of indicator species. Given that our methods are fully transferable, although the information content of putative indicator species likely varies, we anticipate applying the methods to our data on birds and butterflies in the Chesapeake Bay Lowlands. Moreover, we anticipate applying multiple-state occupancy models to selected species of birds and butterflies in the central and western Great Basin. We are eager to explore environmental associations with

abundances of these taxonomic groups at multiple spatial and temporal extents. We also hope to examine whether inferences about extents associated with species richness and beta diversity are consistent with inferences about extents associated with abundance.

We also think it would be feasible and worthwhile to explore how breeding phenology, reproductive success, density, and occupancy of birds in the Great Basin are associated with contemporary and projected variation in weather and climate; and to examine how the interaction of phenological responses to climate and other biological responses to management-driven changes in land cover may affect the feasibility of conserving species of management concern. For example, we could test whether our data on subregional trends in occupancy and abundance are consistent with trends across the Great Basin Bird Conservation Region, and whether trends at either spatial extent are associated with the species' biological traits. It would be straightforward to test whether subregional or Bird Conservation Region-level trends in occupancy and abundance are associated with published climate-change vulnerability rankings. These tests would be of interest and relevance to other researchers and managers given recent development of methods to characterize phenology on the basis of occupancy data. They would address whether local responses to environmental change may be transferable across the Great Basin and whether responses to climate change potentially can be predicted on the basis of life history information. Furthermore, we believe it would be useful to test whether contemporary elevational ranges and temporal shifts in species' elevational ranges are associated with local climate, and whether breeding phenology and reproductive success are associated with extremes, variability, or means of local weather. Moreover, one could test whether the nexus between climate change and proposed vegetation management may affect the breeding phenology or viability of species of concern.

Although the Chesapeake Bay Lowlands and Great Basin are ecologically distinct, some species of songbirds in either region have similar breeding habitat and can be matched phylogenetically. As a result, one can examine how different configurations of vegetation, and different drivers of changes in vegetation structure and composition, are associated with population dynamics of similar species. For example, Hooded Warbler (*Setophaga citrina*) in the Chesapeake Bay Lowlands and MacGillivray's Warbler (*Geothlypis tolmiei*) in the Great Basin both build open-cup nests in shrubs and are associated with deciduous woodlands. As another illustration, Wood Thrush (*Hylocichla mustelina*) in the Chesapeake Bay Lowlands and Cassin's Finch (*Haemorhous cassinii*) in the Great Basin both build cup nests fairly high in trees and are associated with diverse woodlands.

Implementation

We regularly shared data, inferences, reports, and publications with resource managers and wildlife biologists at Fort Eustis, Hawthorne Army Depot, the Marine Corps Mountain Warfare Training Center, and the Naval Facilities Engineering Command's Southwest Central Integrated Project Team; with DoD's federal partners, including the US Fish and Wildlife Service, Bureau of Land Management, US Forest Service, and Great Basin Landscape Conservation Cooperative; and with state and local agencies and citizens' groups. DoD resource managers and their commanding officers indicated that our results would contribute to watershed management programs and Integrated Natural Resources Management Plans. We also responded to the

installations' periodic requests for information on topics such as the ecology and locations where we recorded particular species of rare birds. Additionally, Fort Eustis was interested in related work, supported by other sources, on relations between densities of ticks and white-tailed deer.

Our results may inform not only assessment and monitoring of native species but land use and management actions intended to maintain these species. For example, our work suggests that if maintenance of anurans is a management objective, then conservation of contemporary populations *in situ* may be more effective than restoration or construction of new wetlands. As another illustration, our results suggest that in coastal Virginia, culling of white-tailed deer may increase habitat quality for species of birds that nest in shrubs and glean insect prey from foliage, including several species of conservation concern. We found that it may be useful to include not only larval hostplants but plants that provide nectar for adult butterflies in assessment and monitoring programs for butterflies, and to project how land use (e.g., road maintenance, seeding after disturbances) may affect these aspects of butterfly habitat. More generally, environmental associations with species richness or occupancy of anurans, birds, and butterflies that were identified in our work can be used to project how natural or anthropogenic phenomena that affect these environmental attributes also may affect native species.

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Appendix A. Supporting data

All data collected in the course of this project are being archived.

Data collected in the Chesapeake Bay Lowlands will be deposited in the College of William and Mary's digital archive (<https://digitalarchive.wm.edu>). This archive is the College of William and Mary and Virginia Institute of Marine Science's online repository of research. The archive is an effort to collect, preserve, and distribute digital material related to and produced by the university and its students, faculty, and staff, and is accessible to the public.

Most of the data collected in the Great Basin have been deposited with the Forest Service Research Data Archive (see Appendix B). Data that have not yet been deposited will be added to the archive in the form of new editions of the existing data packages.

Appendix B. Scientific and technical publications

Articles in peer-reviewed journals

- Jirinec, V., R.E. Isdell, and M. Leu. 2016. Prey availability and habitat structure explain breeding space use of a migratory songbird. *The Condor* 118:309-328.
- Jirinec, V., C.P. Varian, C.J. Smith, and M. Leu. 2016. Mismatch between diurnal home ranges and roosting areas in the Wood Thrush (*Hylocichla mustelina*): possible role of habitat and breeding stage. *The Auk* 133:1-12.
- Leu, M., M.L. Farnsworth, E. Fleishman, D.S. Dobkin, R.D. Scherer, B.R. Noon, and B.G. Dickson. 2017. Effects of point-count duration on estimated detection probabilities and occupancy of breeding birds. *Journal of Field Ornithology*, in press.
- Fleishman, E., R.D. Scherer, A. Zapalla, and M. Leu. 2017. Estimation of the occupancy of butterflies in diverse biogeographic regions. *Diversity and Distributions* 23:1–13.
- Yen, J.D.L., J.R. Thomson, J.M. Keith, D.M. Paganin, E. Fleishman, D.S. Dobkin, J.M. Bennett, and R. Mac Nally. In press. Balancing generality and specificity in ecological gradient analysis with species abundance distributions and individual size distributions. *Global Ecology and Biogeography*.
- Fleishman, E., J.D.L. Yen, J.R. Thomson, R. Mac Nally, D.S. Dobkin, and M. Leu. Identifying spatially and temporally transferrable surrogates of species richness. *Ecological Indicators*, in revision.
- Pavlik, D.T., E. Fleishman, R.D. Scherer, and R.B. Blair. Environmental associations with post-fire butterfly occupancy in the Sierra Nevada, California. *Natural Areas Journal*, in review.
- Pavlik, D.T., E. Fleishman, N. Wang, P. Boswell, and R.B. Blair. Sugars in nectar sources and their use by butterflies (Lepidoptera: Hesperioidea and Papilioidea) in the Sierra Nevada, California. *Journal of Research on the Lepidoptera*, in review.

Other publications

- Fogarty, F. and E. Fleishman. 2015. Field guide and natural history of breeding birds on the western edge of the Great Basin. Davis, California. <https://www.serdp-estcp.org/Tools-and-Training/Resource-Conservation-and-Climate-Change/Species-Management>.
- Jirinec, V. 2015. Wood Thrush (*Hylocichla mustelina*) habitat use on the breeding grounds in coastal Virginia. M.S. thesis. College of William and Mary, Williamsburg, Virginia.
- Pavlik, D.T. 2015. Post-fire associations of butterfly behavior, occupancy, and abundance with environmental variables and nectar sources in the Sierra Nevada, California. M.S. Thesis, University of Minnesota, St. Paul.
- Ramos, D.S. 2012. Using a multi-scale life-history approach to explore occupancy patterns of pond-breeding anurans in eastern Virginia. M.S. thesis. College of William and Mary, Williamsburg, Virginia.
- Thompson, M. 2016. Weather-driven changes in occupancy of multiple butterfly species in southeastern Virginia. Undergraduate honors thesis, College of William & Mary, Williamsburg, Virginia.

Zappalla, A. 2016. Factors effecting occupancy and persistence of two common woodland butterfly species of the eastern United States, *Papilio glaucus* and *Eurytides marcellus*. M.S. thesis. College of William and Mary, Williamsburg, Virginia.

Invited presentations

- Fleishman, E. 2012. Discriminating among ecological responses to weather and climate. Great Basin Climate Forum, Reno, Nevada.
- Fleishman, E. 2013. Deriving practical information about management of Great Basin ecosystems from pretty things with wings. Humboldt–Toiyabe National Forest Supervisor's Office, Sparks, Nevada.
- Fleishman, E. 2013. Projecting and detecting species-level responses to variation in weather and changes in climate. Webinar hosted by the Southwest Climate Science Center.
- Fleishman, E. 2014. Fleishman, E., D.S. Dobkin, B.G. Dickson, and M.L. Farnsworth. Detecting and projecting species-level responses to variation in weather and changes in climate. Organized oral session on increasing resilience to climate change and extreme events. Ecological Society of America, Sacramento, California.
- Fleishman, E. 2014. Applications of science to resource management in the western United States. Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile.
- Fleishman, E. 2015. Trade-offs between statistical rigor and biological inferences in the Great Basin and Chesapeake Bay Lowlands. University of Minnesota, St. Paul.
- Fleishman, E. 2015. Resolving multidisciplinary tensions in contemporary wildlife biology. University of Montana, Missoula.
- Fleishman, E. 2015. Applications of remote sensing to ecological monitoring and modeling. Departamento de Ciencias Ecológicas, Facultad de Ciencias, Universidad de Chile.
- Fleishman, E. 2015. Fleishman, E. and D.S. Dobkin. Responses of wildlife habitat to climate variability and fire in sagebrush shrubsteppe and pinyon and juniper woodlands. Symposium on implications of “hotter drought” for forest ecosystems and their management in the southwestern United States. Biennial Conference of Science and Management on the Colorado Plateau and Southwest Region, Flagstaff, Arizona.
- Fleishman, E. 2015. Reconciling statistical rigor and biological inference in occupancy models. University of Connecticut, Storrs.
- Fleishman, E. 2016. Fleishman, E., R. Scherer, M. Leu, and D.T. Pavlik. Reconciling statistical rigor and biological inference in models of butterfly occupancy. Symposium on current insect conservation: research and theory. Pacific Branch, Entomological Society of America, Honolulu, Hawaii.
- Fleishman, E. 2016. Reconciling statistical rigor and biological inference in models of occupancy. Department of Fisheries and Wildlife, Oregon State University, Corvallis.
- Fleishman, E. 2016. Identifying biologically and statistically meaningful levels of organization and sampling for multiple taxa. Workshop on multiscale space and time dynamics of sagebrush and sage-grouse. US Geological Survey, Boise, Idaho.
- Fleishman, E. 2016. Natural history and land management in the western United States. National Taiwan University, Taipei.

- Fleishman, E. 2017. Reconciling rhetoric, statistical rigor, and ecological inference in the Great Basin. Department of Fish, Wildlife and Conservation Biology, Colorado State University, Fort Collins.
- Fleishman, E. 2017. Measuring and interpreting faunal responses to climate in the Intermountain West. Department of Atmospheric Science, Colorado State University, Fort Collins.
- Jirinec V., D.A. Cristol, and M. Leu. 2014. Deer browsing correlates with songbird community change: evidence from surveys in coastal Virginia and the Shenandoah Valley. Annual meeting of the Eastern Shore Chapter of the Virginia Master Naturalists, Melfa, Virginia.
- Leu, M., V. Jirinec, and D. Cristol. 2015. Deer browsing correlates with songbird community change: evidence from surveys in coastal Virginia and the Shenandoah Valley. Quarterly meeting of the Virginia Master Naturalists.
- Leu, M., V. Jirinec, D. Cristol, and M. Teague. 2015. Deer presence correlates with changes in bird assemblages. University of Virginia, Blandy Field Research Station, Boyce, Virginia.
- Pavlik, D.T. 2016. Post-fire associations of butterfly behavior, occupancy, and abundance with environmental variables and nectar sources in the Sierra Nevada, California. Webinar. California Fire Science Consortium.

Contributed presentations

- Fleishman, E., M. Leu, D.S. Dobkin, M. Farnsworth, B.R. Noon, R. Scherer, and J.D.L. Yen. 2016. Comparison of statistically rigorous methods for estimation of avian species richness in the Great Basin. North American Ornithological Conference, Washington, D.C.
- Fleishman, E., M. Leu, M. Farnsworth, and D.S. Dobkin. 2015. Effects of point-count duration on estimated probabilities of detection and occupancy of breeding birds. Joint Meeting of the American Ornithologists' Union and Cooper Ornithological Society, Norman, Oklahoma.
- Jirinec, V. 2013. Does white-tailed deer (*Odocoileus virginianus*) browsing affect forest songbird communities? Annual meeting of the Society for Advancement of Chicanos and Native Americans in Science, San Antonio, Texas.
- Jirinec, V. 2013. Does white-tailed deer (*Odocoileus virginianus*) browsing affect forest songbird communities? Annual meeting of The Wildlife Society, Milwaukee, Wisconsin.
- Jirinec, V. 2015. Mismatch between daytime home ranges and roosting areas in the Wood Thrush: why are males sleeping around? Annual graduate research symposium, College of William & Mary, Williamsburg, Virginia.
- Jirinec, V. and M. Leu. 2014. Wood Thrush microhabitat associations: implications for persistence in a human-modified landscape. Joint meeting of the American Ornithologists' Union, Cooper Ornithological Society, and Society of Canadian Ornithologists, Estes Park, Colorado.
- Leu, M., R. Scherer, K. Watson, and E. Fleishman. 2015. Estimation of occupancy parameters for breeding birds on the basis of single-visit and multiple-visits point-count designs. Joint Meeting of the American Ornithologists' Union and Cooper Ornithological Society, Norman, Oklahoma.

- Niccoli, M. and M. Leu. 2013. Is occupancy modeling a feasible alternative to collecting demography data? Annual meeting of the Wilson Ornithological Society, Williamsburg, Virginia.
- Ramos, D. and M. Leu. 2012. Using occupancy patterns to infer landscape connectivity for breeding anurans. Annual meeting of The Wildlife Society, Portland, Oregon.
- Zappalla, A. 2015. How resource availability influences occurrence of *Papilio glaucus* (eastern tiger swallowtail). Annual graduate research symposium, College of William & Mary, Williamsburg, Virginia.

Poster presentations

- Deverakonda, A., V. Jirinec, C. Smith, and M. Leu. 2015. Determining space use of breeding Wood Thrush (*Hylocichla mustelina*) pairs in southeastern Virginia. Poster. Joint Meeting of the Association of Field Ornithologists, Society of Canadian Ornithologists, and Wilson Ornithological Society, Wolfville, Nova Scotia.
- Jirinec, V. and M. Leu. 2014. Deer browsing correlates with songbird community change: evidence from point count surveys at study sites with contrasting land use. Poster. Ecological Society of America annual meeting, Sacramento, California.
- Niccoli, M. and M. Leu. 2012. Are occupancy models feasible alternatives to collecting demography data? Poster. Fifth North American Ornithological Conference, Vancouver, British Columbia, Canada.
- Pouder, J. 2013. Are human footprint models an adequate tool to predict human stressor on ecological processes? Poster. Annual meeting of The Wildlife Society, Milwaukee, Wisconsin.

Data archived

- Fleishman, E. 2013. Detections of breeding birds in the Shoshone, Toiyabe, Toquima, and Monitor ranges, Nevada. 2nd Edition. Forest Service Research Data Archive, Fort Collins, Colorado. <http://dx.doi.org/10.2737/RDS-2011-0002.2>
- Fleishman, E. 2013. Incidental and long-distance bird observations in the Shoshone, Toiyabe, Toquima, and Monitor ranges, Nevada. Forest Service Research Data Archive, Fort Collins, Colorado. <http://dx.doi.org/10.2737/RDS-2013-0012>
- Fleishman, E. 2013. Presence and absence of butterflies in the Shoshone Mountains and Toiyabe and Toquima ranges, Nevada. 2nd Edition. Forest Service Research Data Archive, Fort Collins, Colorado. <http://dx.doi.org/10.2737/RDS-2011-0003.2>
- Fleishman, E. 2013. Vegetation structure and composition in the Shoshone Mountains and Toiyabe, Toquima, and Monitor ranges, Nevada. Forest Service Research Data Archive, Fort Collins, Colorado. <http://dx.doi.org/10.2737/RDS-2013-0007>
- Fleishman, E. 2015. Detections of breeding birds in the Shoshone, Toiyabe, Toquima, and Monitor ranges, Nevada. 3rd Edition. Forest Service Research Data Archive, Fort Collins, Colorado. <http://dx.doi.org/10.2737/RDS-2011-0002.3>
- Fleishman, E. 2015. Detections of breeding birds in the Wassuk Range, Sweetwater Mountains, and east slope of the Sierra Nevada, Nevada and California. Forest Service Research Data Archive, Fort Collins, Colorado. <http://dx.doi.org/10.2737/RDS-2015-0031>

- Fleishman, E. 2015. Incidental and long-distance bird observations in the Shoshone, Toiyabe, Toquima, and Monitor ranges, Nevada. 2nd Edition. Forest Service Research Data Archive, Fort Collins, Colorado. <http://dx.doi.org/10.2737/RDS-2013-0012-2>
- Fleishman, E. 2015. Incidental and long-distance bird observations in the Wassuk Range, Sweetwater Mountains, and east slope of the Sierra Nevada, Nevada and California. Forest Service Research Data Archive, Fort Collins, Colorado. <http://dx.doi.org/10.2737/RDS-2015-0033>
- Fleishman, E. 2015. Presence and absence of butterflies in the Shoshone Mountains and Toiyabe and Toquima ranges, Nevada. 3rd Edition. Forest Service Research Data Archive, Fort Collins, Colorado. <http://dx.doi.org/10.2737/RDS-2011-0003.3>
- Fleishman, E. 2015. Presence and abundance of butterflies in the Wassuk Range, Sweetwater Mountains, and east slope of the Sierra Nevada, Nevada and California. Fort Collins, CO: Forest Service Research Data Archive. <http://dx.doi.org/10.2737/RDS-2015-0030>
- Fleishman, E. 2015. Vegetation structure and composition in the Shoshone Mountains and Toiyabe, Toquima, and Monitor ranges, Nevada. 2nd Edition. Forest Service Research Data Archive, Fort Collins, Colorado. <http://dx.doi.org/10.2737/RDS-2013-0007-2>
- Fleishman, E. 2015. Vegetation structure and composition in the Wassuk Range, Sweetwater Mountains, and east slope of the Sierra Nevada, Nevada and California. Forest Service Research Data Archive, Fort Collins, Colorado. <http://dx.doi.org/10.2737/RDS-2015-0032>
- Pavlik, D.T. 2016. Presence and absence of butterflies in the Rim Fire, Stanislaus National Forest, California. Forest Service Research Data Archive, Fort Collins, Colorado. <http://dx.doi.org/10.2737/RDS-2016-0021>.
- Pavlik, D.T. 2016. Post-fire vegetation attributes in the Rim Fire, Stanislaus National Forest, California. Forest Service Research Data Archive, Fort Collins, Colorado. <http://dx.doi.org/10.2737/RDS-2016-0020>.